NUTRIENT USE EFFICIENCY IN SIMPLIFIED TROPICAL ECOSYSTEMS

By

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NUTRIENT USE EFFICIENCY IN SIMPLIFIED TROPICAL ECOSYSTEMS

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Nutrient use efficiency, the ratio of plant production per unit of nutrient, is a concept applicable to leaves, plants, and ecosystems. To what extent is nutrient use efficiency at each scale dependent upon that at smaller and larger scales? Nitrogen (N) and phosphorus (P) use efficiencies at all three scales were measured in plantations of three tree species (*Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*), grown alone and in combination with two large-stature, perennial monocots (*Heliconia imbricata* and *Euterpe oleracea*) at La Selva Biological Station, Costa Rica. Nutrient use efficiency was estimated as the ratio of cumulative photosynthesis to total nutrients invested (for leaves); as the ratio of biomass production to nutrient uptake (for plants); and as the ratio of net primary productivity to soil nutrient supply (for ecosystems).

Leaf level N and P use efficiency were highest for *Hyeronima*, which had the longest-lived leaves, even though the highest rates of photosynthesis per unit N were

achieved by *Cedrela*, which had the shortest-lived leaves. Maximum photosynthesis per unit P did not differ among species despite wide interspecific variation in photosynthesis and foliar P. Plant level and ecosystem level N and P use efficiencies were highest for *Hyeronima* and lowest for *Cordia.*

Interspecific patterns of leaf-level nutrient use efficiency for P (but not for N) were maintained through the plant level, but plant-level N use efficiency was influenced by larger-scale factors, possibly soil N availability. Interspecific patterns at the ecosystem level differed from plant-level patterns for both N and P; ecosystem nutrient use efficiency was influenced by changes in relative N and P limitation, a larger-scale phenomenon. Thus, linkages among nutrient use efficiencies at different scales are subject to both top-down and bottom-up controls—the former determined primarily by environment, and the latter determined primarily by the properties of the specific organisms involved.

The interactions between top-down and bottom-up controls on nutrient use efficiency can influence the outcome of interspecific competition, thereby determining species distributions along successional seres and gradients of soil fertility. These interactions can also be important in designing species mixes to achieve high nutrient use efficiency in managed ecosystems.

CHAPTER 1
INTRODUCTION

Steadily, and not so slowly, we are transforming our global landscape—hectare by hectare, year after year. Much of this is occurring in the tropics: people who have been marginalized economically are forced into environments that have limited agricultural potential. All too often the result is deforestation for non-sustainable agriculture, to be succeeded by more of the same on the adjacent hectare a few years later (Leonard 1989, Ramakrishnan 1992b).

How can we stop this seemingly inexorable trend? One way is to improve the well-being of the rural peoples who are otherwise obligated to destroy natural ecosystems in order to earn a livelihood. The design of agro-ecosystems that are economically, socially, politically, and ecologically sustainable is a potent force for conservation. It is, in fact, the only way that society can accommodate growth while conserving its natural heritage.

The fact that vast areas of tropical forest have already been destroyed, coupled with demand for land on which to practice agriculture, signals a tremendous need for restoration. In some cases the goal of restoration should be re-construction of a close facsimile of the original ecosystem—essentially a conservation-based objective; in others the target might be an ecosystem that bears structural resemblance to the original but consists of species useful to people—a sustainable-land-use objective. The two objectives

are complementary, for well-conserved natural ecosystems provide the water and soil resources needed by farmers, just as sustainable agroecosystems alleviate pressures on natural ecosystems.

There is substantial evidence that imitation of forest structure in the design of land use systems can impart desirable ecological traits such as high productivity, resistance and resilience to pest attack, and maintenance of soil fertility (Gliessman et al. 1981, Ewel 1986, Ramakrishnan 1992a, Altieri 1995). The disadvantage of such systems is horticultural complexity, making both management and marketing arduous tasks. The solution to the design of sustainable land use systems for the humid tropics probably lies somewhere between the unmanageable high diversity of the tropical forest and the dangerous simplicity of annual-crop monocultures.

One important limitation to sustainable agriculture is the cost of fertilizer. Nutrients removed during crop harvest must be replenished, and the only natural sources are weathering of parent materials, atmospheric fixation (in the case of nitrogen), atmospheric deposition as rainfall and dust, and, on flood plains, water-borne deposits. If the amounts removed in harvest exceed the sum of those three sources, then farming is tantamount to nutrient mining; the end result is impoverishment of soil and, ultimately, degraded lands that sustain neither people nor forests.

Nutrient use efficiency is a measure of productivity per unit of nutrient available. Just as the label implies, it is a measure of the efficiency with which elements essential for growth are deployed in plants. The concept is useful at several scales, ranging from single leaves to whole plants to entire plant communities. Although it is most widely used in ecological studies, the concept has equal applicability—and, more importantly,

utility—in agro-ecosystems. Agronomists have long been aware of genetic differences in nutrient use efficiency between species, and indeed between cultivars of the same species (Marschner 1995). They have taken advantage of differences in nutrient use efficiency to breed cultivars that tolerate deficiencies, particularly of micronutrients (Brown and Jones 1977), and to breed cultivars that have high uptake efficiency to better utilize applied fertilizer in intensive cropping systems (Schenk and Barber 1979, Mengel 1983). There is now a growing recognition of the need to select for cultivars that would have a high efficiency of nutrient uptake and use on low-fertility soils (Gabelman and Gerloff 1983, Dambroth and El Bassam 1990, Sauerbeck and Helal 1990). Farmers who are able to manage plant nutrients in ways that are conservative, effective, and efficient have a greater likelihood of sustaining their efforts than those whose use of limiting nutrients is wasteful, ineffective, and inefficient. The applicability of nutrient use efficiency may be of greatest value in tropical countries, where manufactured fertilizers are disproportionately expensive and where degraded lands are often the starting point for agricultural development.

Nutrient Use Efficiency

Historically, numerous indices have been used to estimate plant nutrient use efficiency (Table 1-1). These range from estimates at the individual leaf level to estimates at the level of the whole community. In addition, these indices encompass a range of time scales, from instantaneous measures to those that integrate across processes occurring over many years. Direct comparisons among nutrient use efficiency indices are problematic because determinations of productivity (the numerator) and nutrient

availability (the denominator) vary among indices. At the plant level, for example, the numerator is estimated variously as total plant biomass (Chapin 1980, Shaver and Melillo 1984), annual foliage production (Ågren 1983), and wood and leaf mass produced (Boerner 1984). Similarly, at the community level, the denominator is estimated as the total amount of nutrients lost from plants or the rate at which they are stored within plants (Vitousek 1982, Waring and Schlesinger 1985), annual nutrient return to the soil (Gray 1983), and nutrients available to plants from resorption and mineralization (Lennon et al. 1985).

What, then, are appropriate measures of nutrient use efficiency at several scales that would allow a comparison of parallel physiological and ecological processes occurring at these scales? I suggest that nutrient use efficiency be measured as the ratio of total productivity to nutrients available for achieving that productivity, at each scale of measurement. Thus, at the leaf level, nutrient use efficiency is the ratio of net carbon accrued by a leaf over its lifetime to the amount of nutrients invested in that leaf; at the plant level nutrient use efficiency is the ratio of biomass produced to total nutrients taken up (Hirose 1975); and at the stand level nutrient use efficiency is the ratio of total stand biomass production to total nutrients available for uptake from the soil.

Leaf nutrient use efficiency

The maximum photosynthetic rate that can be achieved for a certain leaf nutrient content, referred to as potential photosynthetic nutrient use efficiency (PPNUE; Field and Mooney 1986), is the most commonly used measure of nutrient use efficiency at the leaf level. Hereafter, it is referred to as potential PNUE. Although not ecologically realistic—leaves seldom photosynthesize at their maximum rates for sustained periods of

time—potential PNUE nonetheless serves as an index for comparing potential performance among species.

Maximum photosynthetic rates increase linearly with both leaf nitrogen (Field and Mooney 1986) and phosphorus (Reich and Schoettle 1988) content, but there is a high variance associated with these relationships. Interspecific differences in partitioning of foliar nutrients to photosynthetic and non-photosynthetic functions is one source of variation in the photosynthesis-foliar nutrient relationship (Field and Mooney 1986). A further source of variation in the photosynthesis-foliar nutrient relationship comes from interspecific differences in partitioning of foliar nitrogen related to photosynthetic functions into RuBP carboxylase and thylakoid proteins. For example, plants in low irradiance environments invest a higher proportion of leaf nitrogen in the apparatus for light capture than in the apparatus for carbon fixation (Evans 1989) and therefore have lower potential photosynthetic nutrient use efficiency compared to plants that grow in full sun.

Another source of variation in the photosynthesis-foliar nutrient relationship is interspecific variation in leaf lifespan (Field and Mooney 1986). Long lived leaves tend to be more sclerophyllous (Turner 1994) with greater allocation to carbon-rich protective tissue at the expense of photosynthetic tissue, thereby constraining photosynthetic capacity.

Given the various factors that can affect potential PNUE, a more ecologically realistic measure of leaf nutrient use efficiency is cumulative carbon gain by a leaf over its lifetime for the total nutrients invested in that leaf, hereafter referred to as cumulative PNUE. Cumulative carbon gain by a leaf depends not only on photosynthetic capacity but

also on the time over which that photosynthesis occurs—the leaf's lifespan. Greater leaf longevity can compensate for low rates of photosynthesis, thereby leading to high cumulative carbon gain per unit of leaf nutrient over the lifespan of a leaf (Chabot and Hicks 1982). The total nutrient investment in a leaf—equivalent to nutrients lost from the plant at the end of the leaf's lifespan—is the sum of nutrients leached by stemflow and throughfall as a result of rain washing over leaves, and nutrients not resorbed prior to leaf abscission. This measure does not account for nutrients invested in a leaf over its lifetime and resorbed by the plant prior to abscission. Nonetheless, it is a measure of cumulative carbon gain by a leaf as a function of total nutrients that are irretrievable invested in a leaf over its lifespan.

One measure of cumulative PNUE is "potential photosynthate," which is the product of light saturated net photosynthetic rate, leaf duration, and the fraction of nutrients retained at the time of leaf abscission (Small 1972). This is a more integrated measure than potential PNUE, but again, it is ecologically unrealistic. As the label implies, it is a measure of the photosynthesis a leaf may potentially carry out, but over the course of its life there may be a great deal of variation in a leaf's photosynthetic capacity (Field and Mooney 1983, Harrington et al. 1989, Ackerly and Bazzaz 1995). What is more, on a daily basis some portion of a leaf's carbon gain is expended as dark respiration. A more suitable measure of a leaf's lifetime nutrient use efficiency is the ratio of daily net carbon gain integrated over the leaf's life (to account for changes with leaf age), to the fraction of nutrients lost via leaching and at the time of leaf abscission.

Plant nutrient use efficiency

In the simplest sense, plant nutrient use efficiency can be expressed as the ratio of plant biomass to plant nutrient content (Chapin 1980, Chapin and Van Cleve 1989). This ratio is equivalent to the inverse of plant nutrient concentration. In the case of perennials, however, this measure is complicated by tissue and nutrient losses over a plant's lifetime due to leaf abscission, herbivory, and foliar leaching. Nutrient use efficiency estimated in this manner neglects nutrients that are taken up and used to produce biomass but are subsequently lost, due either to leaching from foliage or to leaf abscission, thereby *overestimating* nutrient use efficiency. Conversely, this measure disregards the proportion of nutrients in the plant that comes from internal recycling, for instance due to resorption at the time of leaf abscission, thereby *underestimating* nutrient use efficiency. In perennials, therefore, resource utility, which is the ratio of the total rate of biomass production to the total rate of nutrient uptake, is a better measure of nutrient use efficiency (Hirose 1975). Total nutrient uptake can be determined by adjusting net uptake (measured as nutrient content at the time of sampling) for nutrient resorption and nutrient losses via litterfall and foliar leaching.

Nutrient use efficiency at the plant level depends on the efficiency with which plants use the nutrients that they have taken up, and the efficiency with which nutrients taken up are retained to be re-used within the plant. A more formal statement of this idea is provided by Berendse and Aerts (1987), who propose that nutrient use efficiency be considered as the product of nutrient productivity and mean residence time of nutrients in the plant. Nutrient productivity is biomass produced per unit nutrient per unit time. Mean residence time is related to longevity—whether of the plant as a whole, or of a particular

plant part—and to the efficiency with which nutrients are retained in the plant at the time of tissue abscission (Shaver and Melillo 1984, Birk and Vitousek 1986).

There may be evolutionary tradeoffs between selection for traits that lead to higher nutrient productivity and those that lead to longer nutrient residence times (Aerts 1990). Rapid growth is generally accompanied by rapid tissue turnover and entails high rates of nutrient acquisition and loss. Rapid leaf turnover is necessary to avoid self-shading and to maintain high photosynthetic rates (Field 1983, Field and Mooney 1986, Schmid and Bazzaz 1994), for example. Conversely, greater tissue longevity and longer nutrient retention within the plant seem to preclude rapid growth. Thus, the same nutrient use efficiency may be achieved by one of several means.

It has been suggested that high fertility environments select for higher nutrient productivity (Aerts 1990). In such environments, the ability to grow rapidly, even if it means faster turnover of acquired nutrients, confers an advantage: individuals that grow bigger faster can capture more of the available nutrient pool than their competitors. In low fertility environments, in contrast, longer nutrient residence times may be an advantage, even though plants with higher nutrient productivity show more rapid initial growth (Aerts and van der Peijl 1993). In such environments, the ability to retain nutrients once they have been acquired, even at the cost of reduced growth rates, is potentially more beneficial: every molecule of nutrient discarded is a molecule potentially lost to uptake and sequestration by competitors.

Ecosystem nutrient use efficiency

The most widely used index of ecosystem nutrient use efficiency is the ratio of litterfall mass to litterfall nutrient content (Vitousek 1982), hereafter referred to as the

litterfall index of nutrient use efficiency. This index is applicable to mature communities at steady-state: litterfall mass is assumed to be equivalent to net productivity, and litterfall nutrient content is assumed to reflect net nutrient uptake. A larger ratio of litterfall mass to litterfall nutrient content therefore reflects greater net productivity per unit of nutrient uptake and results from more conservative nutrient use by plants comprising the community. This measure has also been related to the tightness with which nutrients are cycled through the system (Vitousek 1984). A larger ratio of litterfall mass to litterfall nutrient content indicates a low nutrient return to the soil per unit of litterfall and results in less potential loss from the system (e.g., by leaching from the soil). Comparisons across a range of tropical and temperate ecosystems, using this index, indicate a pattern of greater efficiency in the use of nutrients when there are less nutrients for plant uptake (Vitousek 1982, 1984; Cuevas and Medina 1986; Silver 1994; Bridgham et al. 1995).

The litterfall index of nutrient use efficiency suffers from several drawbacks. One drawback is that it does not account for nutrient losses via canopy leaching (Grubb 1989). The magnitude of nutrients leached in throughfall may range from 10-20% and 0-15% of total losses of phosphorus and nitrogen, respectively (Parker 1983). Nutrients leached from foliage must be replenished by uptake from the soil. If nutrient uptake is not adjusted for nutrient leaching losses, the result is an overestimate of nutrient use efficiency. Another drawback of the litterfall index of nutrient use efficiency is that biomass and nutrient losses to herbivores are not accounted for. Herbivores consume, on average, about 10 percent of community leaf biomass annually (Coley and Barone 1996). Where herbivores feed selectively on nutrient-rich tissues, their impact on nutrient use efficiency may be disproportionately large relative to biomass consumed.

The litterfall index of nutrient use efficiency has another limitation when making comparisons across communities: there is an implicit assumption that allocation of biomass to leaves, stems, and roots is invariant from one community to another, when in fact proportional allocation to different tissues can vary with nutrient availability. First, differences in fertility can alter relative allocation to roots and shoots, thereby affecting calculations of nutrient use efficiency (Aerts and Caluwe 1994). At the community level, above-ground productivity increases with soil fertility, but below-ground productivity can be higher (Keyes and Greier 1981, Ostertag 1998) or lower (Nadelhoffer et al. 1985, Ostertag 1998) on infertile soils than on more fertile sites (though the evidence is confounded by differences in methodology; Hendricks et al. 1993). Furthermore, though little is known about the carbon costs of supporting mycorrhizal associations, it is likely that on infertile soils there is greater mycorrhizal activity—and greater belowground allocation of carbon to support mycorrhizal associations—than on fertile soils (Johnson et al. 1997). Community productivity estimated solely on the basis of above-ground litterfall could therefore either overestimate or underestimate the unseen component of productivity occurring below ground, leading to an erroneous estimate of nutrient use efficiency.

In addition to altering relative allocation to above- and below-ground tissue, differences in soil fertility also affect the partitioning of above-ground tissue into stems and leaves. A forest on infertile soil may put more biomass into leaf tissue than into stem tissue compared to a forest on more fertile soil (Grubb 1977). The resultant nutrient use efficiency of these two forests, if estimated as total dry mass produced per unit of nutrient, is the opposite of nutrient use efficiency estimated as the ratio of litterfall mass

to litterfall nutrients, because of the lower nutrient concentration of woody tissue (Grubb 1989).

As an alternative to the litterfall index of nutrient use efficiency, therefore, ecosystem level nutrient use efficiency may be characterized as the ratio of total productivity to the rate of soil nutrient supply. This ratio depends on the efficiency with which the individual species making up the community use nutrients that they take up to produce biomass, and the efficiency with which the community as a whole takes up available nutrients from the soil.

Cross-Scale Linkages in Nutrient Use Efficiency: A Theoretical Model

Are there linkages between nutrient use efficiency at various scales? Holling (1992) suggested that ecological systems are characterized by hierarchies of organization governed by processes operating at distinct spatial and temporal scales—in particular, that processes at higher scales operate independently of those at smaller scales. Others contend that physiological processes operating at the scale of the organism feed into larger scale processes such as biogeochemical cycling (Field and Ehleringer 1993), and that bottom-up scaling is necessary to understand the mechanisms controlling processes at higher scales (Dawson and Chapin 1993).

There are a number of problems inherent in scaling processes from one level to another. Variation observed at a particular scale may or may not be relevant to processes at the scale above it. For example, in comparing photosynthetic carbon gain by leaves and canopies, minute to minute variation in photosynthetic rates measured on an individual leaf has little relevance to daily, integrated net carbon gain by the canopy as a whole. The

reverse also holds: at larger spatial and temporal scales processes interact with the environment in ways not apparent at smaller scales of measurement. For example, within a canopy, leaves acclimate to changing light environments over time scales of days and weeks. This response would not be obvious from short-term measurements on individual leaves alone.

Nutrient use efficiency is an index of physiological and ecological function, and is applicable to processes at scales ranging from leaves to whole communities. In seeking to design sustainable land use systems and restore degraded lands, high nutrient use efficiency is a desirable attribute at every scale of endeavor: long lived leaves are better protected against herbivores (Turner 1994); plants that have a high nutrient use efficiency can be relatively productive, even on impoverished soils; and stands that have tight nutrient cycles are potentially more buffered against losses of soil fertility (Shaver and Melillo1984). Understanding how nutrient use efficiency scales from one level to the next, therefore, could be invaluable in efforts to design sustainable land use systems and restore the functional properties of degraded lands. In the following sections I propose a theoretical model relating leaf, plant, and stand nutrient use efficiency. Following that, I outline an empirical approach for testing these relationships.

From potential to cumulative leaf nutrient use efficiency

At the level of an individual leaf one can consider a leaf's potential PNUE (i.e., the PPNUE of Field and Mooney [1986]; for a description of the symbols used in the equations that follow, see Table 1-2)

$$Potential\ PNUE = \frac{P_{MAX}}{L_N} \quad (1)$$

As mentioned earlier, potential PNUE serves as a good index for comparing potential performance among species, but when considering parallel measures of nutrient use efficiency by leaves and plants, it is ecologically more realistic, hence more useful, to consider a leaf's cumulative PNUE.

Cumulative PNUE is the ratio of the total net carbon assimilated by a leaf over its lifespan to total nutrients invested in that leaf (i.e., the fraction of nutrients in the leaf that is lost to the plant via foliar leaching, or in litterfall at the time of leaf abscission). A portion of net carbon assimilation and foliar nutrients is lost to herbivory, but those losses are not treated in the derivation that follows. The numerator of the cumulative PNUE expression is net photosynthesis integrated over leaf lifespan. The denominator is the sum of nutrients lost via foliar leaching and nutrients lost as litter (i.e., the fraction of foliar nutrients not resorbed at the time of leaf abscission).

$$Cumulative\ PNUE = \frac{\int^{LIFESPAN} P_S}{(L_N \times (1-RES)) + LEACH} \quad (2)$$

Assuming a linear decline in photosynthesis with leaf age (Zotz and Winter 1994, Ackerly and Bazzaz 1995), the numerator can be denoted by the product of average daily net photosynthesis and leaf lifespan:

$$Cumulative\ PNUE = \frac{P_S^* \times LIFESPAN}{(L_N \times (1-RES)) + LEACH} \quad (3)$$

This equation can be rearranged as shown in equation 4. The first term of the expression now becomes the ratio of average daily net photosynthesis to leaf nutrient content. By analogy with equation 1, this is the leaf's daily photosynthetic nutrient use efficiency (PNUE). The second term of the expression is the ratio of leaf lifespan to the fraction of nutrients lost by the plant when that leaf is shed.

$$Cumulative\ PNUE = \frac{P_s^*}{L_N} \times \frac{LIFESPAN}{(1-RES) + \frac{LEACH}{L_N}} = PNUE \times \frac{LIFESPAN}{(1-RES) + \frac{LEACH}{L_N}} \quad (4)$$

Thus a leaf's cumulative PNUE depends not only on the efficiency with which foliar nutrients are used for photosynthesis, but also on leaf lifespan, nutrient resorption, and some measure of "leakiness" (i.e., vulnerability to nutrient leaching).

From the leaf to the plant

At the plant level, nutrient use efficiency is the ratio of total biomass produced to total nutrients taken up (Hirose 1975):

$$Plant\ NUE = \frac{\Delta W}{\Delta N} \quad (5)$$

The two parts of this expression, total biomass produced and total nutrients taken up, can be separately derived as shown in the following sections.

Derivation of the numerator, ΔW. Over short time scales, the change in biomass of a plant (i.e., net assimilation) is the difference between net carbon gain by leaves and respiration by non-photosynthetic tissues. Net daily carbon assimilation by leaves is the product of net daily photosynthesis per unit leaf area and total leaf area.

Respiration by non-photosynthetic tissue is the product of shoot and root mass and shoot and root respiration, respectively. The rate of change in biomass is, therefore,

$$\frac{dW}{dt} = P_S\,(LA) - R_S\,(SW) - R_R\,(RW) \tag{6}$$

Net photosynthesis per unit leaf area can be denoted by the product of net photosynthesis per unit leaf nutrient and leaf nutrients per unit leaf area, to express photosynthesis in terms of photosynthetic nutrient use efficiency, as follows (Lambers et al. 1990).

$$P_S = \frac{P_S}{L_N} \times L_N = PNUE \times L_N = PNUE \times \frac{LNC}{SLA} = PNUE \times LNC \times SLM \tag{7}$$

There is some justification for treating the crown as a "big leaf" with respect to photosynthetic nutrient use efficiency (Kull and Jarvis 1995), even though photosynthetic capacity itself varies from leaf to leaf with differences in age and position. The hypothesis is that light absorption and photosynthetic nutrient use efficiency are maximized by the crown as a whole; there is evidence in partial support of this hypothesis, though the underlying mechanisms are yet unclear (Terashima and Hikosaka 1995). First, within leaves, reorientation of the chloroplasts in the palisade and spongy cells of the mesophyll and altered ratios of chlorophyll a to b lead to more efficient light absorption; second, among leaves, foliar nutrient reallocation leads to more efficient nutrient use by the crown as a whole: canopy photosynthesis is higher than it would be if nutrients were homogeneously distributed through the crown (Terashima and Hikosaka 1995). This nutrient reallocation has been alternately explained on the basis of optimization of foliar nutrients (Field 1983, Hirose and Werger 1987) or acclimation to

changing light environments within the crown (Kull and Jarvis 1995). Profiles of foliar nutrient content should therefore match profiles of integrated light availability through the crown (Field 1983, Hirose and Werger 1987, Kull and Jarvis 1995), i.e., as lower leaves are increasingly more shaded, foliar nutrients are reallocated to leaves in high light environments. Observed gradients of foliar nutrients do, in fact, approximate predicted patterns of foliar nutrient distribution in plant crowns, although the theoretical optimal gradient is always steeper than the observed gradient (Terashima and Hikosaka 1995). Most studies on nutrient gradients within plant crowns have been done on herbaceous species (Field 1983, Hirose and Werger 1987), but there have been studies on trees as well (e.g., DeJong and Doyle 1985). Based on this reasoning, the expression for photosynthesis derived in equation 7 can be substituted into equation 6 to denote photosynthetic carbon assimilation by the whole crown (Lambers et al. 1990), regardless of differences in individual leaf photosynthetic capacities:

$$\frac{dW}{dt} = (PNUE \times LNC \times SLM)\,(LA) - R_S\,(SW) - R_R\,(RW) \tag{8}$$

where LA (leaf area), SW (shoot biomass), and RW (root biomass) are each a function of time. Integrating equation 8 therefore, we get:

$$\Delta W = (PNUE{\cdot}LNC{\cdot}SLM)(LA_0 + \Delta LA) - R_S(SW_0 + \Delta S) - R_R(RW_0 + \Delta R) \tag{9}$$

Derivation of the denominator, ΔN. Total nutrient uptake in a given time is the sum of the increase in standing stock of nutrients in the plant and nutrient losses from the plant, over that time. The increment in standing stock of nutrients can be expressed as the product of total new biomass accrued and nutrient concentration of that biomass. Nutrient

losses are the sum of losses in herbivory, litterfall, and leaching from plant tissue. Herbivory losses are not dealt with further in the derivation that follows. Nutrient losses in above-ground litter can be expressed as the product of litterfall mass, peak leaf nutrient content, and the fraction of leaf nutrients not resorbed by the plant (i.e., the inverse of the fraction of nutrients resorbed by the plant). Leaching losses can be expressed as the product of nutrients leached per unit leaf area and the total leaf area of fallen litter. The assumption here is that the bulk of nutrient leaching is from mature, senescing leaves, when leaves are most susceptible to nutrient losses via leaching (Tukey 1970). Nutrient losses in below-ground litter can be expressed as the product of litter mass and root nutrient concentration, assuming negligible nutrient resorption from fine roots prior to abscission (Nambiar 1987).

$$\begin{aligned}\Delta N &= \Delta L \cdot LNC + \Delta S \cdot SNC + \Delta R \cdot RNC + LIT \cdot L_N \cdot SLA(1 - RES) + LIT \cdot SLA \cdot LEACH + RLIT \cdot RNC \\ &= \Delta L \cdot LNC + \Delta S \cdot SNC + \Delta R \cdot RNC + LIT \cdot L_N \cdot SLA((1 - RES) + LEACH / L_N) + RLIT \cdot RNC \end{aligned} \quad (10)$$

Equations 9 and 10 denote total plant biomass production and total plant nutrient uptake, respectively. Combining them gives us an expression for plant nutrient use efficiency:

$$\begin{aligned} Plant\ NUE &= \frac{\Delta W}{\Delta N} \\ &= \frac{(PNUE \cdot LNC \cdot SLM)(LA_0 + \Delta LA) - R_S(SW_0 + \Delta SW) - R_R(RW_0 + \Delta RW)}{\Delta L \cdot LNC + \Delta S \cdot SNC + \Delta R \cdot RNC + LIT \cdot L_N \cdot SLA((1 - RES) + \frac{LEACH}{L_N}) + RLIT \cdot RNC} \end{aligned} \quad (11)$$

As can be seen from equation 11, nutrient use efficiency at the plant level is affected both by processes at the leaf level and by processes at the plant level. Biomass production depends on the efficiency with which leaves assimilate carbon for the total nutrient

investment in leaf tissue. It also depends on total allocation to photosynthetic tissue relative to non-photosynthetic tissue. A plant that invests proportionally more photosynthate (and consequently, nutrients) in leaf tissue is likely to have greater carbon return per unit nutrient invested at the whole plant level than one that invests more photosynthate in root tissue (Bloom et al. 1985, Chapin et al. 1987).

Leaf characteristics, in addition to being linked with biomass production at the plant level, influence nutrient retention within plants. Long-lived leaves are associated with reduced rates of nutrient losses from plants (Monk 1966, Escudero et al. 1992, Aerts 1995), a proposed explanation for the dominance of evergreens in low fertility environments (Monk 1966, Chabot and Hicks 1982, Aerts 1995). Greater within-plant nutrient retention may also be achieved by more efficient nutrient resorption at the time of leaf abscission (Shaver and Melillo 1984, Birk and Vitousek, 1986). There is some evidence for more efficient resorption in nutrient-poor habitats (Miller et al. 1976, Turner 1977, Boerner 1984, Vera and Cavelier 1994), although the evidence is confounded by differences in species composition between habitats; there is some evidence for the opposite phenomenon as well (Lennon et al. 1985, Birk and Vitousek 1986, Chapin and Moilanen 1991, Nambiar and Fife 1991).

From the plant to the stand

Nutrient use efficiency at the stand level is defined as the ratio of net primary productivity to the rate of soil nutrient supply:

$$Stand\ NUE = \frac{NPP}{SUPPLY} \tag{12}$$

Nutrient use efficiency at the stand level is really a composite of two indices: (i) the efficiency with which nutrients taken up by the component species are utilized for biomass production, and (ii) the efficiency with which available nutrients are taken up and thereby prevented from being leached from the system. Thus, equation 12 can be further expanded so that the ratio of net primary productivity to soil nutrient supply is equivalent to the product of biomass produced per unit of nutrient uptake and nutrient uptake per unit of nutrient supplied by the soil (see Bridgham et al. 1995):

$$Stand\ NUE = \frac{NPP}{SUPPLY} = \sum_i \frac{\Delta W_i}{\Delta N_i} \times \frac{\Delta N_i}{SUPPLY} \tag{13}$$

where *i* denotes the number of species making up the stand. In a stand comprising more than one species, individual species' nutrient uptake would be affected by interactions among species (e.g. interspecific competition) and therefore equation 13 may be better expressed as:

$$Stand\ NUE = \frac{NPP}{SUPPLY} = \sum_i \frac{\Delta W_i}{\Delta N^*_i} \times \frac{\Delta N^*_i}{SUPPLY} \tag{14}$$

where ΔN^* denotes species' nutrient uptake resulting from interspecific interactions in comparison with ΔN, which denotes nutrient uptake in the absence of interspecific interactions.

It follows that increased ecosystem nutrient use efficiency is possible under one of three scenarios (or some combination of the three). First, if the component species have high plant-level nutrient use efficiencies (i.e., biomass produced per unit of nutrient taken up), then the ratio of total biomass production to total nutrient uptake by the stand would

be greater than by a stand of species with low nutrient use efficiencies. This, then, would represent a direct relationship between nutrient use efficiency at the plant and stand scales.

A second way in which high ecosystem level nutrient use efficiency could be achieved is if the stand as a whole had a high nutrient uptake efficiency. The ability of plants to take up available nutrients depends on root physiology, root architecture, and the extent to which roots explore the soil volume (Caldwell and Richards 1986). In addition, a mixture of species may have greater resource uptake than a species grown alone. This can happen if (i) species are temporally separated in their peak demand for resources (Rao 1986, Fukai and Trenbath 1993), (ii) there is spatial separation in species' root systems (Huck 1983), or (iii) species take up resources in different proportions (e.g., mixtures of legumes and non-legumes; Martin and Snaydon 1982).

The third possible situation under which there can be higher ecosystem nutrient use efficiency is if a high productivity is achieved in spite of decreased nutrient supply, e.g., due to feedbacks from litter quality, affecting rates of decomposition, and consequently, nutrient supply. Such a situation could occur in communities composed of species that resorb a large proportion of nutrients before leaf abscission, or in communities composed of species with long-lived leaves. High within-plant nutrient retention leads to poor quality litter and therefore low rates of decomposition and nutrient supply (Schlesinger 1991). Greater leaf longevity has also been related to low rates of litter decomposition (Gower and Son, 1992): long lived leaves tend to be sclerophyllous, possibly to provide greater protection over an individual leaf's lifespan (Turner 1994);

such leaves make tough litter that breaks down slowly (Aber and Melillo 1982, Melillo et al. 1982).

Cross-Scale Linkages in Nutrient Use Efficiency: An Empirical Approach

How best can we mimic the functional properties of complex natural ecosystems in the design of agro-ecosystems that are biologically sustainable, yet horticulturally manageable? Similarly, how can we best restore nutrient-cycling and productivity characteristics of ecosystems on degraded and abandoned landscapes? We are faced with questions about processes at scales of the ecosystem, or the landscape, and constrained by our need to answer these questions based on our knowledge of processes at smaller spatial and temporal scales.

The issue of linkages across scales raises both philosophical and practical questions. If, as Holling (1992) suggests, processes at different scales are independent of one another and are governed by distinct suites of factors, then there is little that we can infer about the functioning of ecosystems based on what we know about the species making up those ecosystems. Similarly, there are limits to what we can infer about the interactions among individuals, based on our knowledge of differences in their morphology and physiology.

Nutrient use efficiency at the leaf, plant, and stand scales may be subject to variation in factors operating independently of one another. For instance, leaf nutrient use efficiency may change from minute to minute as light and humidity vary, causing changes in photosynthesis, without that having any bearing on growth and productivity at the plant and stand levels, respectively. Similarly, seasonal variation in temperature and

rainfall may influence rates of litter breakdown, consequently soil nutrient supply, but have little direct affect on leaf nutrient use efficiency. Nevertheless, there may be linkages between processes at each of these scales, as proposed in the previous section. A better understanding of these linkages would enable us to select for a high efficiency of nutrient use at several scales.

At the leaf level, potential PNUE is a function of maximum photosynthetic capacity and foliar nutrient content (equation 1). High photosynthetic capacity is associated with short-lived leaves, as was mentioned earlier (Reich et al. 1992). As leaf longevity increases, so too does the need to invest a greater proportion of foliar nutrients in functions related to longevity (Field and Mooney 1986) thereby taking away from investment in photosynthetic apparatus. Therefore, I predict that

1. Potential PNUE is inversely related to leaf longevity.

One explanation for the existence of long-lived leaves is that they occur in environments where resources are scarce and nutrients, once acquired, need to be conserved within plants (e.g., Chapin 1980). Such leaves have low photosynthetic capacity, but their greater longevity may be a means of achieving similar, or greater, cumulative carbon assimilation per unit of foliar nutrient over the lifespan of individual leaves (equation 3). This leads to the prediction that

2. Cumulative PNUE increases with leaf longevity.

At the plant level, nutrient use efficiency is a function of biomass production and nutrient uptake (equation 11). Biomass production depends on the efficiency with which leaves assimilate carbon for the total nutrient investment in leaves—a link between nutrient use efficiency at the leaf and plant scales—and the relative allocation to

photosynthetic, as opposed to non-photosynthetic, tissue. Nutrient uptake is affected by a plant's ability to conserve nutrients once taken up, itself affected by leaf longevity and nutrient resorption—another link between nutrient use efficiency at the leaf and plant scales. Therefore, I predict that

3. Patterns of cumulative nutrient use efficiency among species at the leaf level should be consistent with patterns of nutrient use efficiency among species at the plant level.

At the stand level, nutrient use efficiency is a composite of two indices, nutrient use efficiency of the individuals that constitute the stand—a link between nutrient use efficiency at the plant and stand scales—and the nutrient uptake efficiency of the stand as a whole (equation 13). For stands comprising single species, I predict that

4. Patterns of nutrient use efficiency at the plant level are consistent with patterns of nutrient use efficiency at the stand level.

Uptake efficiency depends on total nutrient uptake, given a certain rate of soil nutrient supply. A higher uptake can be achieved a variety of ways, whether due to species' differences in resource requirements, or due to spatial and temporal separation in species' requirements for resources. I predict, therefore, that

5. Greater nutrient uptake by a stand will lead to a higher nutrient use efficiency at the stand level.

These predictions were investigated in a series of simplified tropical ecosystems comprising replicated monoculture and polyculture plantations at La Selva Biological Station, Costa Rica (Chapter 2). The monocultures are of three tree species; the polycultures consist of the same three tree species co-planted with individuals of a very different lifeform—large, perennial monocots.

The three tree species represent a range of resource use characteristics at the leaf and the whole plant level. Thus they provided a useful system in which to investigate nutrient use efficiency at several scales. In addition, the monocultures and polycultures provided an opportunity to investigate nutrient use efficiency at the stand level in stands that differed in diversity. The study site and species are described in greater detail in chapter 2. The relationship between leaf-level characteristics and nutrient use efficiency at the leaf level forms the subject of chapter 3; nutrient use efficiency at the plant level forms the subject of chapter 4; and nutrient use efficiency at the stand level forms the subject of chapter 5. The links between nutrient use efficiency at several scales are examined in chapter 6, along with their implications for the design and restoration of managed ecosystems.

Table 1-1. Indices of nutrient use efficiency at various scales. Adapted and modified from Grubb (1989).

Measure-ment Scale	Index	Definition	Source
leaf	Photosynthetic production	saturation net photosynthetic rate x leaf duration x nitrogen retention fraction	Small 1972
	Potential photosynthetic nutrient use efficiency	maximum photosynthetic rate / foliar nutrient content	Field and Mooney, 1986
plant	Resource Utility	net dry matter production / amount of resource absorbed	Hirose 1975
	Nutrient use efficiency	1 / tissue nutrient concentration	Chapin 1980
	Nitrogen productivity	annual yield of foliage / unit of nitrogen in the foliage	Ågren 1983
	Nitrogen and phosphorus growth efficiency	wood and leaf mass produced / nitrogen or phosphorus lost in litterfall	Boerner 1984
	Uptake efficiency	increase in plant N or P mass / N or P mass available	Shaver and Melillo 1984
	Recovery efficiency	(mass of N or P per unit area of mature leaves) - (mass of N or P per unit area of dead leaves) / (mass of N or P per unit area of mature leaves)	Shaver and Melillo 1984
	Use efficiency	plant biomass / plant N or P mass	Shaver and Melillo 1984
	Nitrogen use efficiency	nitrogen productivity x mean residence time of nitrogen in the plant	Berendse and Aerts 1987
community	Litterfall nutrient use efficiency	total biomass lost from plants or stored within plants / total nutrients lost from plants or stored within plants	Vitousek 1982
	Nutrient use efficiency quotient	annual canopy production of dry matter / annual nutrient return to the soil	Gray 1983
	Production efficiency	aboveground biomass production / nutrient uptake	Waring and Schlesinger 1985
	Nitrogen use efficiency	aboveground biomass production / nutrient available (from resorption and mineralization)	Lennon et al. 1985

Table 1-2. Terms used in the derivation of the equations, and the units in which they are expressed.

Term	What it denotes	Units
LA	leaf area	m^2
LEACH	foliar nutrients lost via leaching	g / m^2
LIFESPAN	leaf lifespan	d
LIT	biomass of above-ground litter	g
L_N	leaf nutrients on an area basis	g / m^2
LNC	leaf nutrients on a mass basis	g / g
LW	leaf biomass	g
ΔL	change in leaf biomass	g
ΔLA	change in leaf area	m^2
NPP	net primary productivity	$g . m^{-2} . d^{-1}$
ΔN	nutrient uptake	g
P_{MAX}	maximum net photosynthesis	$\mu mol . m^{-2} . s^{-1}$
PNUE	daily photosynthetic nutrient use efficiency	$g . mol^{-1} . d^{-1}$
P_S	daily net photosynthesis	$g . m^{-2} . d^{-1}$
P_S^*	average daily net photosynthesis	$g . m^{-2} . d^{-1}$
RES	fraction of foliar nutrients resorbed	(dimension less)
RLIT	biomass of below-ground litter	g
RNC	root nutrients on a mass basis	g / g
R_R	root respiration rate	$g . g^{-1} . d^{-1}$
R_S	shoot respiration rate	$g . g^{-1} . d^{-1}$
RW	root biomass	g
ΔR	change in root biomass	g
SLA	specific leaf area	m^2 / g
SLM	specific leaf mass	g / m^2
SNC	shoot nutrients on a mass basis	g / g
SUPPLY	rate of soil nutrient supply	$g . m^{-2} . d^{-1}$
SW	shoot biomass	g
ΔS	change in shoot biomass	g

Table 1-2. (Continued)

dW/dt	plant growth rate	g / d
ΔW	change in plant biomass	g

CHAPTER 2
STUDY SITE AND SPECIES

Study Site

This research was conducted in experimental plantations at La Selva Biological Station in the Atlantic lowlands of Costa Rica. La Selva pertains to Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). Mean annual temperature at La Selva is 25.8 °C and average yearly rainfall is approximately 4 m, with a brief dry season from February to April. Even during the dry season, mean monthly rainfall is seldom less than 0.1 m (Sanford et al. 1994), and there is ample warmth and moisture for rapid growth, year-round.

The experimental plantations are on a level alluvial terrace at about 41 m above sea level, on a peninsula formed by two of the three rivers that border La Selva, Río Sarapiquí and Río Puerto Viejo. The soil profile shows several distinct depositional sequences (Haggar and Ewel 1994), though the site was not flooded by the two highest floods in recent memory (1970 and 1996).

The soil at the site is a eutric Hapludand—an andesitic soil of humid climates, with minimum horizon development and high base saturation (Weitz et al. 1997). In the surface horizon the soil is a sandy loam (0-15 cm depth) giving way to sandy loam-silty loam (down to about 50 cm; Haggar and Ewel 1994). The soil is well drained, with low bulk density (0.67 g/cm^3) and high organic matter content (Table 2-1). Soil at the site is

relatively rich in extractable nitrogen (N) and phosphorus (P) and has high base saturation dominated by calcium (Table 2-1). In addition to relatively high base saturation and extractable P, values of KCl-extractable N at the site (13.7 μg/g , soil depth 0-10 cm) were high compared with values reported from a range of other sites in the neotropics and the Pacific (4.1-12.6 μg/g, soil depth 0-15 cm; Vitousek and Matson 1988). It is widely held that P is among the soil nutrients that most limits plant production in the tropics while N tends to be more limiting to plant production in the temperate zone (Vitousek 1982, 1984). At this site, however, values of extractable N and P are both high relative not only to the older, upland soils at La Selva, but also in comparison with other regions of the humid tropics (Table 2-2).

When it was annexed to La Selva in the mid-1980s, the site was a recently abandoned cacao plantation. In early 1991, the site was cleared; the overstory trees—mainly *Cordia alliodora*—were harvested for timber; the slash was then burned; and the experimental plantations were established immediately thereafter.

Species

The three tree species used in this study—*Cedrela odorata* L. (Meliaceae), *Cordia alliodora* (R. & P.) Cham. (Boraginaceae) and *Hyeronima alchorneoides* Allemão (Euphorbiaceae)—are all native to Costa Rica and occur in the forest at La Selva or in abandoned pastures and secondary vegetation in the neighboring region. All three species are fast-growing tropical hardwoods.

Cedrela odorata (hereafter, *Cedrela*) is confamilial with the true mahoganies (*Swietania* spp.) and like mahogany, is highly prized for its timber. In its natural range it

extends from southern Mexico to Peru and Argentina, and to the West Indies to Trinidad and Tobago. It is widely planted in the neotropics and has been introduced to parts of Africa and south-east Asia (Glogiewicz 1998). To a lesser extent, it is also planted as an overstory tree with coffee (Glover and Beer 1986) and in managed fallows (Hammond 1995). In plantations, it very rarely escapes attack from a shoot-borer moth, *Hypsipila grandella* (Whitmore 1978), and considerable genetic and silvicultural research on increasing the resistance of *Cedrela* and other Meliaceae to *Hypsipila* is underway (Newton et al. 1993).

Cordia alliodora (hereafter, *Cordia*), like *Cedrela*, is distributed widely in the neotropics and extends from central Mexico to northern Argentina and the islands of the Caribbean. It is valued for its durable timber, and has been planted extensively since the early part of this century, both in its native range and in Africa and the Pacific region (Greaves and McCarter 1990). *Cordia* is fast-growing, and it readily colonizes fertile soils. In Costa Rica it is used for reforestation (Butterfield 1994) and as an overstory tree in combination with coffee and cacao (Glover and Beer 1986, Somarriba and Beer 1987).

Hyeronima alchorneoides (hereafter, *Hyeronima*) is a massive canopy emergent in the forests at La Selva and can attain a height of up to 50 m (Hartshorn and Hammel 1994). It has dense, durable wood. For a tree that has such dense wood, *Hyeronima* is remarkably fast-growing as a juvenile under high light conditions—growing as much as 3 m a year—although it may take several hundred years to reach its full size in the forest (Clark and Clark 1992). Of the three tree species, it has been the least studied, though it is becoming better known as a species with potential to be used in reforestation (Butterfield and Espinoza 1992, Butterfield 1994).

The three species were chosen for their very different phenologies and architectures—above and below ground—thus representing an array of resource capture and resource use characteristics. *Cedrela* has monopodial growth, with orthotropic branches that form an open crown. It has large, pinnately compound leaves that can be up to a meter long, with 10-20 pairs of leaflets, each about 40 cm^2. At La Selva, *Cedrela* tends to be deciduous during the dry season (February-April). *Cordia*, like *Cedrela*, has monopodial growth, but with plagiotropic branches that are produced in whorls, creating an open, tiered crown. It has small, simple leaves, each about 30 cm^2. Once it reaches reproductive maturity *Cordia* loses its leaves during the wet season (around July at La Selva); as a juvenile, it maintains its foliage year-round, although it is partially deciduous during the dry season. *Hyeronima* has sympodial growth with orthotropic branches that form a dense crown. *Hyeronima* is evergreen, with very large, simple leaves as a juvenile (area ~280 cm^2); the tree produces progressively smaller leaves as it ages, such that emergent trees in the forest have leaves that are only about 60 cm^2. By age 2 yr in the experimental plantations, *Hyeronima* stands had developed a dense canopy, with a high leaf area index and very little light penetration to the understory, compared to the more open canopies of *Cordia* and *Cedrela* (Table 2-3; Haggar and Ewel 1995).

In addition to differences in architecture, leaf morphology, and phenology, the species also differ greatly in foliar nutrient concentrations. Although N and P concentrations in leaves of all three species are high (due, no doubt, to the fertile soils of the study site), concentrations also differ markedly among species, as was manifest at the outset of the experiment: at age 2 yr *Cordia* had higher foliar N concentrations (3.39 percent), than the other two species (2.90 and 2.76 percent for *Cedrela* and *Hyeronima*,

respectively). In contrast, foliar P concentrations were higher in *Hyeronima* (0.35 percent) than in *Cordia* (0.27 percent) or *Cedrela* (0.22 percent). Furthermore, ratios of litterfall to standing leaf biomass indicate a substantially shorter leaf lifespan, consequently more rapid biomass and nutrient turnover, for *Cedrela* and *Cordia* relative to *Hyeronima* (Haggar and Ewel 1995; see also Chapter 3).

The relative differences among the three species in their architecture above ground are also reflected in their architecture below-ground. *Hyeronima* has the densest, most compact root system. *Cordia*, in contrast, has a laterally extensive root system, and *Cedrela* is intermediate between the other two species. Of the three species, *Hyeronima* allocates the greatest amount of biomass to fine roots and has the highest fine root length density (Table 2-3). Of the remaining species, *Cordia* has the higher fine root length density, due to its high specific root length, despite not differing greatly from *Cedrela* in biomass allocation to fine roots (Haggar and Ewel 1995). The species' differences in root morphology is likely to affect their relative uptake of different soil nutrients: *Hyeronima*, with roots that explore the soil intensively may be more effective at uptake of phosphorus, an immobile soil nutrient; *Cordia*, on the other hand, with roots that explore the soil extensively, is likely to have higher uptake of nitrogen, a mobile soil nutrient (Haggar and Ewel 1994). Foliar nutrient concentrations for the three species support this hypothesis.

The remaining species used in this study, a palm and a perennial herb, are representatives of the second most abundant lifeform in forests of the region—large, perennial monocots. The palm, *Euterpe oleracea* Mart (Arecaceae), or açaí, occurs widely over northern South America, though it is best known from Brazil, where it is one

of the most abundant species in frequently inundated, fertile floodplain forests of the lower Amazon basin. It is a tall (about 20 m), multi-stemmed palm, with pinnate fronds, that rapidly colonizes disturbed, swampy areas (Henderson 1995). In Brazil it is an economically important species, harvested for its fruit and heart of palm, as well as for a number of other subsistence uses. Its management includes planting in home gardens and the silvicultural management of natural regeneration (Anderson 1988).

The second monocot, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae), is a large (up to 3 m tall), perennial, banana-like herb, with red bracts subtending hummingbird-pollinated flowers on its 0.5 m long inflorescences. Like other members of the genus, it is a vegetatively reproducing herb with monocarpic ramets that readily colonizes gaps and is commonly found in young secondary vegetation (Stiles 1979). At La Selva, it is abundant in the secondary growth around the plantations, forming dense clumps with numerous basal shoots and large, vertically displayed leaves with leaf blades up to 2 m in length.

Experimental Design

In early 1991, plantations (40 x 60 m) of *Cedrela*, *Cordia*, and *Hyeronima* were established in a randomized block design with three replicates (Figure 2-1). The 40 x 60 m plantations were divided into equal halves (40 x 30 m). One half was left as the tree monocultures; the other half was under-planted with palms and heliconias in an additive design to create polycultures. The monoculture plantations were used to investigate linkages in nutrient use efficiency at the leaf, plant, and stand scales by the three tree species. The monoculture and polyculture plantations were used to investigate nutrient

use efficiency by stands that differed in diversity: stands comprising a single lifeform—trees, compared to stands comprising two lifeforms—trees, and large, perennial monocots.

In each plot trees were planted in rows 1.73 m apart. Within rows, individuals were spaced at 2 m intervals; individuals in successive rows were offset by a meter. The resulting planting pattern has each tree at the center of a hexagon, 2 m from its six closest neighbors. The overall density was 2887 trees per ha, which is several times greater than is normal for these species in forestry plantations. The reason for the high planting density was to ensure that resource acquisition and productivity were maximized early in stand development. In the polyculture plots palms were planted in alternate rows, in alternate spaces between trees, i.e., at one-fourth the tree density. Heliconias were planted in rows that were not planted with palms, in every available space between trees, i.e., at half the tree density.

Table 2-1. Soil characteristics measured in the surface 10 cm at the time of plantation establishment (Haggar and Ewel 1994, 1995). Values are means (standard deviation).

pH	Organic Matter (%)	Extractable N (µg/g)	Bicarbonate Extractable P (µg/g) †			Exchangeable Bases (Cmol$_c$/kg)‡		
			inorganic	organic	microbial	Ca	Mg	K
6.5	5.9 (1.2)	13.7 (0.8)	46.0 (4.4)	19.4 (4.4)	18.1 (5.0)	15.9 (5.5)	3.2 (0.7)	1.7 (0.4)

†Phosphorus extractions were done on soils sampled from 0-15 cm.
‡Values for Ca, Mg and K are from soils sampled in 1993.

Table 2-2. Soil characteristics of the study site as compared with other regions of the humid tropics.

Soil Type	Vegetation	Depth (cm)	pH	Organic Matter (%)	Exchangeable Bases ($Cmol_c/kg$)			Extract-able P (µg/g)‡	Source
					Ca	Mg	K		
Eutric Hapludand	**Study Site**	**0-10**	**6.5**	**5.9**	**15.9**	**3.2**	**1.70**	**14.4**	
Typic Tropohumult	Forest, Costa Rica	0-18	5.0	7.13	0.59	0.46	0.35	0.6	Sollins et al. 1994
Andic Humitropept	Forest, Costa Rica	0-26	4.3	11.93	0.79	0.92	0.42	1.7	
Typic Acrustox	Secondary Forest, Brazil	0-10	5.0	3.24†	0.42	0.32	0.15	-	USDA Soil Survey Staff 1975 (ibid)
Oxic Dystrandept	Pasture, Maui, Hawaii	0-20	6.2	8.87†	17.5	6.3	1.70	-	
Typic Eutrandept	Cultivation, Maui, Hawaii	0-23	6.7	5.81†	35.8	11.7	6.10	-	
Typic Dystropept	Puerto Rico	0-15	4.2	2.28†	1.60	0.70	0.30	-	
Typic Eutropept	Puerto Rico	3-15	5.0	1.77†	13.2	0.40	0.40	-	
Haplic Acrorthox	Forest, Brazil	0-4	4.1	2.76†	0.07	0.09	0.08	-	
Plinthic Orthoxic Tropudult	Secondary Forest, Nigeria	0-7	4.6	0.91†	0.90	0.40	0.10	4.5	Green-land 1981
Psammentic Tropaquent	Secondary Forest, Nigeria	0-15	6.4	5.06†	26.1	2.6	0.4	10.8	
Orthoxic Tropohumult	Rubber Plantation, Nigeria	0-16	4.2	3.88†	3.30	0.70	0.30	6.2	

† organic carbon (%), ‡ acid ammonium fluoride extraction

Table 2-3. Leaf and root characteristics (at age 2 yrs) that affect above and belowground resource capture by the three tree species. Values of specific leaf area and specific root length are means (ranges); values of leaf area index and root length density are means (standard errors) of three blocks. (Modified from Haggar and Ewel 1995.)

Species	Leaves		Fine Roots†	
	Specific Leaf Area cm^2 / g	Leaf Area Index	Specific Root Length m / g	Root Length Density‡ mm / cm^3
Hyeronima	133 (120-150)	6.09 (0.19)	7.2 (5.2-12.0)	4.84 (0.63)
Cedrela	157 (135-190)	1.57 (0.13)	14.1 (5.2-25.6)	0.42 (0.11)
Cordia	148 (136-170)	2.78 (0.68)	20.0 (10.3-35.0)	1.31 (0.27)

† Diameter < 2 mm.
‡ At soil depth of 0-10 cm.

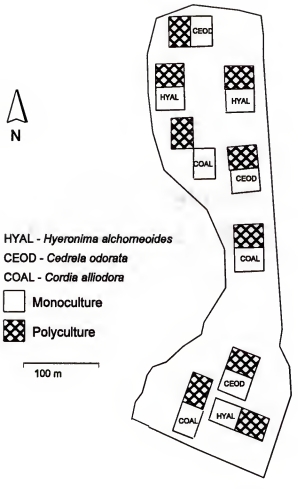

Figure 2-1. Map of the study site showing replicate monoculture and polyculture plantations of the three species.

CHAPTER 3
NUTRIENT USE EFFICIENCY AT THE LEAF LEVEL

Introduction

The efficiency with which plants use nutrients can determine their ability to persist in a given environment. For instance, individuals better at retaining nutrients that they have taken up dominate in low-nutrient environments, even though species with high growth rates and low nutrient retention may grow larger and faster, and consequently dominate initially (Aerts and van der Peijl 1993). Furthermore, differences in nutrient uptake and use efficiency can affect the outcome of interspecific competition (Rundel 1982, Tilman et al. 1997).

A number of investigators have used different measures of species' nutrient use efficiency to characterize distribution patterns across large scale environmental gradients, concluding that plant communities on less fertile soils have lower rates of nutrient return in litterfall than those on more fertile soils (Vitousek 1982, 1984, Silver 1994). Others have described finer scale patterns in species occurrence. For example, differences in nutrient resorption (Gray 1983, Schlesinger et al. 1989) and potential photosynthesis per unit of nutrient invested in leaves (Small 1972) have been suggested as explanations for the spatial distribution of species within a given environment. Similarly, differences in nutrient acquisition and use (Chiba and Hirose 1993) and photosynthetic nutrient use efficiency (Ellsworth and Reich 1996) have been proposed as explanations that underlie

the sequence of species dominance at different stages of primary and secondary succession, respectively.

Previous explanations for these patterns have rested largely on species' differences in leaf habit, i.e., whether species are deciduous or evergreen. It has been suggested that evergreens have slower rates of nutrient turnover (Monk 1966) coupled with lower nutrient requirements (Chabot and Hicks 1982), higher nutrient resorption (Gray 1983, Schlesinger et al. 1989, DeLucia and Schlesinger 1995), and potentially greater photosynthetic production for a certain nutrient investment in leaves (Small 1972, Chabot and Hicks 1982, DeLucia and Schlesinger 1995). Implicit in these explanations is the idea that evergreens, by virtue of their greater (presumed) tissue longevity, have longer nutrient storage times and greater cumulative photosynthetic production per unit of nutrient invested in them (Chapin 1980), as well as lower rates of nutrient losses from the plant (Aerts 1995). But this evergreen-deciduous dichotomy stems largely from a temperate zone bias, because leaf longevity and leaf habit may be quite unrelated—a plant can have very short-lived leaves, yet be an evergreen (Kikuzawa 1991, Craine and Mack 1998). Reich et al. (1991, 1992, 1997) showed that leaf longevity—rather than leaf habit—is a more fundamental axis along which to draw species comparisons. They demonstrated that leaf lifespan is correlated with a number of leaf structural and functional traits, as well as with growth characteristics at the plant level (Reich et al. 1992). Moreover, these patterns hold across a broad range of species and biomes (Reich et al. 1997).

Given the assertion that there is a global convergence in leaf lifespans in response to environmental selection (Reich et al. 1997) and that leaf lifespan is causally related to

other structural and functional leaf characteristics (e.g., specific leaf mass, and mass-based photosynthesis and foliar nutrient contents; Reich et al 1992), can we expect leaf nutrient use efficiency to vary with leaf lifespan in a manner analogous to other leaf characteristics? And by extension, can leaf nutrient use efficiency be used as an index of the environment in which a species is most likely to succeed?

For individual leaves, the most widely used index of nutrient use efficiency is potential photosynthetic nutrient use efficiency (PPNUE; Field and Mooney 1986), hereafter referred to as potential PNUE. This is an instantaneous measure of nutrient use efficiency, and is calculated as the ratio of potential maximum photosynthesis to foliar nutrient content. Although plants seldom photosynthesize at maximum rates for extended periods of time, potential PNUE is a useful index for comparing potential performance among species (Field and Mooney 1986). Maximum photosynthesis is linearly related to foliar nitrogen (Field and Mooney 1986) and phosphorus (Reich and Schoettle 1988). The photosynthesis-nitrogen relationship is linear—within species and among species—when both are expressed on a mass basis, although the relationship can be quite variable among species when photosynthesis and foliar nitrogen are expressed on an area basis (Evans 1989). This variability may be due to differences in leaf longevities and consequent constraints on photosynthetic capacity, or to differences in partitioning of foliar nutrients to photosynthetic and non-photosynthetic functions (Field and Mooney 1986, Evans 1989).

In addition to potential PNUE, which is an instantaneous measure of leaf nutrient use efficiency, it is possible to consider a leaf's cumulative photosynthetic nutrient use efficiency, hereafter called cumulative PNUE, which is the ratio of total carbon

assimilation by a leaf to total nutrient investment in that leaf over its lifetime (cf Small 1972, Rundel 1982). Total carbon assimilation by a leaf depends on its photosynthetic rate as well as the time over which photosynthesis occurs, i.e., the leaf's lifespan. Nutrient investment in a leaf that is subsequently lost from the plant depends on the efficiency with which nutrients are resorbed prior to leaf abscission. Cumulative PNUE is therefore a more integrative measure of leaf nutrient use efficiency, one that combines photosynthetic nutrient use efficiency with characteristics such as leaf lifespan and nutrient resorption.

The selective pressures that lead to higher potential PNUE may be different from the selective pressures that lead to higher cumulative PNUE. It has been demonstrated that leaf lifespan is inversely related to rates of maximum photosynthesis (Reich et al. 1992). In longer-lived leaves, photosynthetic apparatus per unit of leaf mass may be diluted due to the presence of a greater amount of carbon-rich tissue (e.g., tissue with a high proportion of fibers and tannins [Coley 1988]; Williams et al. 1989). In addition, in longer lived leaves there may be a greater allocation of nutrients to non-photosynthetic functions (Field and Mooney 1986). I predict, therefore, that potential PNUE is inversely related to leaf lifespan. Long lived leaves, on the other hand, may have low rates of photosynthesis, but their greater longevity may be a result of selection for maximizing carbon gain per unit of nutrient invested in leaves over their lifespan. I predict, therefore, that cumulative PNUE increases with increasing leaf longevity.

I measured potential PNUE and cumulative PNUE in three species of tropical trees in experimental plantations at La Selva Biological Station in Costa Rica (Chapter 2). The three species, *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora*,

though all fast-growing, differ greatly in their patterns of biomass allocation and rates of leaf turnover (Haggar and Ewel 1995). *Cedrela* and *Cordia,* with rapid leaf turnover are similar to other, early successional tropical tree species; *Hyeronima,* with slower leaf turnover, is more similar to species that occur later in succession (Shukla and Ramakrishnan 1984, Haggar and Ewel 1995). Based on the predictions made above, I hypothesized that *Cedrela* and *Cordia* would have higher potential PNUE, whereas *Hyeronima* would have higher cumulative PNUE. Leaf nutrient use efficiency was measured both with respect to nitrogen (N) and with respect to phosphorus (P). The species were grown under uniform conditions, which ensured that any variation in leaf nutrient use efficiency observed can be attributed to inherent differences in their leaf characteristics, rather than to phenotypic responses to differing environments.

Methods

Maximum Potential Photosynthetic Rate

Potential photosynthetic nutrient use efficiency is denoted as

$$\textit{Potential PNUE} = \frac{P_{max}}{L_N} \qquad (1)$$

where P_{max} is the rate of maximum photosynthesis, and L_N is foliar nutrient content. Maximum potential photosynthetic rates were measured on well-lit, young, fully expanded leaves in the canopy, from atop a movable scaffold tower, in two of the three blocks of the experiment (Chapter 2) during June-July 1997. Permanent tower bases in each plot enabled access to between three and five trees at a time. Photosynthesis was

measured on 10 leaves selected at random at each tower location, making sure that not more than five leaves were from any one individual. The same leaves were then sampled for determination of specific leaf mass and for tissue nutrient analysis.

Photosynthesis was measured using a LI-6200 portable photosynthesis system (LiCor Inc. Lincoln, Nebraska, USA), with an artificial light source (Mini-Cool AC/DC lamp, model #LK 2050) to ensure that light was above saturating levels (>1,600 $\mu mol\ m^{-2}\ s^{-1}$) at all times. In addition to being limited by light, maximum photosynthesis can be limited by stomatal conductance; to eliminate this potential variable, photosynthesis was measured at a standard leaf internal carbon dioxide (CO_2) concentration for all three species. This was achieved by measuring the response of photosynthesis to changing internal CO_2 (A-C_i curves). CO_2 in the leaf cuvette was elevated artificially to above 1200 ppm by blowing into it. Photosynthesis was measured after every 100 ppm drop in chamber CO_2. A-C_i curves obtained by draw-down of CO_2 correlate well with steady-state measurements (McDermitt et. al. 1989).

Maximum potential photosynthetic rates were estimated from the A-C_i curves at a leaf internal CO_2 concentration of 240 ppm for all three species. A standard leaf internal CO2 concentration of 240 ppm was chosen, because under ambient conditions C3 plants tend to adjust stomatal opening to maintain leaf internal CO_2 concentrations close to that value (Wong 1979). Linear regression was used on the linear, ascending portion of the curves to interpolate photosynthetic rate at an internal CO_2 concentration of 240 ppm. The interpolated value of photosynthesis was used to calculate potential PNUE.

Cumulative Photosynthetic Carbon Gain

Cumulative photosynthetic nutrient use efficiency can be depicted as

$$Cumulative\ PNUE = \frac{\int^{Lifespan} P_S}{L_N\ (1-Resorption)} \quad (2)$$

where the numerator is daily photosynthetic carbon gain integrated over the leaf's life. The denominator is the amount of nutrients invested in a leaf over its lifespan and then lost from the plant, i.e., the product of foliar nutrient content and the fraction of nutrients not resorbed prior to leaf abscission.

Photosynthesis as a function of light availability was measured using a LI-6200 portable photosynthesis system (LiCor Inc. Lincoln, Nebraska, USA), with a LiCor dual red-blue light (Quantum Devices Q-Beam 6205 BD) as the light source. Photosynthesis was measured while stepping photosynthetically active radiation (PAR) down from a starting value of ~1,800 μmol m^{-2} s^{-1}. All measurements were made at chamber CO_2 of 330-340 ppm, relative humidity of 60-80% and leaf temperature of 25-37 °C.

Non-rectangular hyperbolas (Thornley 1976) of the form

$$P = [(\alpha I + P_{max}) - \sqrt{(\alpha I + P_{max})^2 - 4\theta\alpha I P_{max}}\ ]/2\theta \quad (3)$$

were fitted to the photosynthesis-light response curves using the non-linear regression procedure in SigmaPlot (SPSS Inc. 1997). P is photosynthetic rate, I is photon flux density, P_{max} is light-saturated photosynthetic rate, α is quantum yield (i.e., the initial slope of the photosynthesis-light response curve) and θ is a term that denotes curvature.

For these calculations, θ was constrained between 0.5 and 0.8; α was given a value of 0.05 μmol CO_2 / μmol photons.

Average daily net carbon assimilation by young and old leaves (in mmol m^{-2} d^{-1}) was calculated using the light response curves and Bigelow's (1998) PAR data. PAR was logged at half-hourly intervals by sensors mounted above the canopy. PAR data used were the average of half-hourly measurements taken on 6 consecutive days in June 1995. Cumulative photosynthesis was then calculated by integrating average daily photosynthesis over leaf lifespans using a decreasing, linear function as follows:

$$\int^{Lifespan} P_S = \int^{Lifespan} f(t)dt \tag{4}$$

$$where\ f(t) = \frac{(P_{S_{old}} - P_{S_{young}})}{(Age_{old} - Age_{young})}\ t + P_{S_{young}} \tag{5}$$

P_{Syoung} and P_{Sold} denote average daily photosynthesis by young and old leaves, respectively; Age_{old} - Age_{young} denotes the age difference between young and old leaves in days; and t denotes time in days. The assumption of a linear decline in photosynthesis with leaf age was based on observations of the decline in photosynthetic capacity with leaf age for other fast-growing tropical trees (Zotz and Winter 1994, Ackerley and Bazzaz 1995).

To estimate the rate of decline in photosynthesis with leaf age, photosynthesis was measured on five young and five old leaves. Leaf position was used as a surrogate for leaf age, which assumes that rates of leaf production are constant, and is an assumption that was based on observations of continuous leaf flushing year-round (except in the case of *Cedrela* during the months of February to April, when it is deciduous). "Young" leaves

were the youngest, fully expanded leaf closest to the growing tip on each branch. "Old" leaves were distal to young leaves and were selected to represent approximately two-thirds of leaf lifespans. For example, if, on average, there were 10 fully expanded leaves per branch, then the sixth leaf from the growing tip was selected to be an "old" leaf. The age of older leaves was estimated as the fraction of total leaf lifespan they represented, in this case 60% of total leaf lifespan. The rate of decline in photosynthesis was calculated as the difference in average daily carbon assimilation by young and old leaves, divided by the length of time over which the decline had occurred (equation 5). Photosynthesis was measured in June 1998, from a scaffold tower in one block of the experiment only. Measurements were made on five branches selected at random, taking care to ensure that the branches sampled came from at least three trees. In the case of *Cordia*, two of the five older leaves had photosynthetic rates that were indistinguishable from rates measured on young leaves. It is possible that the more complex phyllotaxy of *Cordia* precluded selection of similar-aged leaves based on leaf position unlike *Cedrela* and *Hyeronima* that have simpler, sequential phyllotaxy.

Leaf Lifespan

Leaf lifespans of the three species were measured over a 9-month period in two of the three blocks of the experiment, starting in July 1994. Successive cohorts of leaves were tethered and were then censussed periodically until all tethered leaves had abscised, to calculate an average leaf lifespan per cohort.

Leaves were reached by means of a movable scaffold tower. Thirty newly emerged leaves (leaflets, in the case of *Cedrela*) per cohort were tethered with monofilament. Care was taken to ensure that not more than ten leaves were from any one

individual. Previously marked cohorts were censussed each time a new cohort was tethered—every three weeks in the case of *Cedrela,* and every six weeks in the case of *Cordia* and *Hyeronima*. In the case of *Cordia*, monofilament tethers were replaced with wire tethers after tagging the initial couple of cohorts, when it was suspected that node-dwelling ants (Opler and Janzen 1983) may be cutting the tethers, consequently influencing measurements.

Foliar Nutrient Content and Specific Leaf Mass

Leaves used for construction of the A-C_i curves were subsequently sampled for foliar nutrient analysis and to measure specific leaf mass. Leaf lamina disks, of diameter 0.25 cm^2, were punched out from between veins to avoid fibrous tissue (Medina 1984). Disks were dried to constant weight at 70 ^{0}C and weighed. Specific leaf mass was calculated as the ratio of disk mass to disk area. The disks were then digested following a Kjeldahl protocol, and total N and P were analyzed on an autoanalyzer using standard procedures (Alpkem 1986). These foliar nutrient contents were used to calculate both potential and cumulative PNUE.

Potential PNUE was calculated as the ratio of potential maximum photosynthetic rate (in $\mu mol\ m^{-2}\ s^{-1}$) to foliar N and P content (in mol m^{-2}), respectively. Cumulative PNUE was calculated as the ratio of photosynthetic carbon gain over leaf lifespans (in mol m^{-2}), to the product of foliar N and P content (in mol m^{-2}) and the fraction of N and P not resorbed from leaves, respectively. Nutrient resorption was calculated as the difference in nutrient content of living leaves and of freshly fallen litter, expressed as a proportion of nutrient content of living leaves (Chapter 4).

Rates of photosynthesis, foliar nutrient contents, and photosynthetic nutrient use efficiency were analyzed by one-way analysis of variance, with species as the main effect. Analyses were performed using the GLM procedure in SAS (SAS Institute 1988). Interspecific differences in mean photosynthetic rates, foliar nutrient contents, and nutrient use efficiencies were tested using contrasts within the GLM procedure.

Results

Potential Photosynthetic Nutrient Use Efficiency

The response of photosynthesis to elevated leaf internal CO_2 reached an asymptote at a concentration of about 800 ppm for all three species (Figure 3-1). The maximum photosynthetic rate attained was higher for *Cordia* (>30 μmol m^{-2} s^{-1}) than for *Cedrela* and *Hyeronima* (20-25 μmol m^{-2} s^{-1}). Interpolated values of photosynthesis corresponding to a leaf internal CO_2 concentration of 240 ppm expressed on a leaf area basis followed a pattern of *Cordia* > *Cedrela* > *Hyeronima* (Table 3-1), although species differences in photosynthetic rate were not significant ($p = 0.18$). Interpolated values of photosynthesis expressed on a leaf mass basis, however, differed significantly among species ($p = 0.005$), and followed a pattern of *Cedrela* > *Cordia* > *Hyeronima*.

Foliar N concentrations for the three species ranged from about 3 to 4% by weight (Table 3-1). When expressed on a leaf mass basis, *Hyeronima* had a lower foliar N concentration than the other two species ($p = 0.015$), and there was no difference in foliar N concentration between *Cedrela* and *Cordia*, but when expressed on a leaf area basis, *Cordia* had a significantly higher foliar N concentration than the other two species ($p = 0.023$). This difference in relative amounts of foliar N among species, when expressed

variously on mass and area bases, reflects their differences in specific leaf mass—the thick leaves of *Cordia* have more foliar N per unit leaf area than the thinner leaves of *Cedrela* and *Hyeronima*.

Foliar P concentrations for the three species were between about 0.20 and 0.35% by weight (Table 3-1). On a mass basis, foliar P concentrations differed significantly among species ($p = 0.015$); *Cedrela* had a higher foliar P concentration than the other two species, but there was no difference in foliar P concentration between *Hyeronima* and *Cordia*. On an area basis, interspecific differences in foliar P disappeared ($p = 0.17$). Again, this is a reflection of the lower specific leaf mass of *Cedrela*, when compared to the other two species—a high concentration of P on a mass basis is spread over a larger area in the thin leaves of *Cedrela* than in the thicker leaves of *Cordia* and *Hyeronima*.

Potential photosynthetic N use efficiency ranged from about 40 to 60 μmol CO_2 $[mol\ N]^{-1}\ s^{-1}$, and differed significantly among species ($p = 0.004$). *Cedrela* had the highest potential photosynthetic N use efficiency, followed by *Hyeronima*, and then *Cordia* (Figure 3-2). Potential photosynthetic P use efficiency was approximately 1550 μmol CO_2 $[mol\ P]^{-1}\ s^{-1}$ and did not differ among species ($p = 0.99$; Figure 3-3 [a]), despite there being a one-and-a-half fold interspecific variation in both foliar P and photosynthesis (Figure 3-3 [b]).

Cumulative Photosynthetic Nutrient Use Efficiency

Daily courses of photosynthesis for young and old leaves (Figure 3-5) were plotted using the photosynthesis light response curves (Figure 3-4) and half-hourly PAR data. Average carbon gain by young and old leaves, calculated by summing

photosynthesis over a 24 hr period, ranged from about 190 mmol m^{-2} d^{-1} for older *Hyeronima* leaves to 391 mmol m^{-2} d^{-1} for young *Cordia* leaves (Table 3-2).

All three species showed a decline in daily carbon gain with increasing leaf age. The rate of decline was greatest for *Cedrela,* and least for *Hyeronima* (Table 3-2). The age difference between young and old leaves was approximated using the fraction of lifespan represented by old leaves (~ 61, 68, and 71% of total lifespan for *Hyeronima*, *Cedrela*, and *Cordia*, respectively). Cumulative photosynthetic carbon gain by leaves of the three species, calculated by integrating average daily carbon gain over leaf lifespans, varied more than two-fold among species and ranged from about 16 (*Cedrela*) to 37 (*Hyeronima*) mol m^{-2} (Table 3-2).

Cumulative PNUE was calculated using cumulative carbon gain over leaf lifespans, peak foliar nutrient contents, and the fraction of nutrients lost at the time of leaf abscission. The fraction of nutrients lost at the time of leaf abscission by *Cordia* (63% N, 76% P) was higher than for *Cedrela* (50% N, 57% P) and *Hyeronima* (49% N, 59% P), although these differences were not significant (Chapter 4). Cumulative PNUE differed significantly among species ($p = 0.015$ and $p = 0.014$, for N and P, respectively). With respect to both N and P, cumulative PNUE was highest for *Hyeronima*; *Cedrela* and *Cordia* showed no difference in cumulative PNUE (Figures 3-6, 3-7).

Discussion

Components of Nutrient Use Efficiency

Leaf lifespans of the three species (50, 99 and 176 days for *Cedrela*, *Cordia*, and *Hyeronima*, respectively) are at the low end of leaf lifespans reported for a range of

tropical tree species (between 60 d and 4 yr; Reich et al. 1991). Leaf lifespans calculated from turnover rates using leaf standing crop and annual litterfall were correlated with, but longer than, measured lifespans (about 134, 168 and 245 d for *Cedrela*, *Cordia*, and *Hyeronima*, respectively; Chapter 4). It is possible that tethering and handling of leaves shortened their lifespans, or that litterfall- and leaf mass-based calculations overestimated leaf lifespan. Based on lifespans estimated by tagging leaves, maximum photosynthetic rates of the study species were lower than those of species with similar leaf longevity in the Reich et al. (1991) data set, but were equivalent to rates for species of similar leaf longevity (Reich et al. 1991) when using leaf lifespans estimated from turnover rates as the basis for comparison. This indirectly supports the hypothesis that measured lifespans were shortened by the measurement process.

Photosynthetic rates, when expressed on a leaf mass basis, were inversely related to leaf lifespan. This negative relationship between photosynthesis and leaf lifespan is as would be predicted, assuming that longer lived leaves tend to be more sclerophyllous (Turner 1994), and have proportionally more carbon-rich protective tissue (Coley 1988) at the expense of photosynthetic tissue per unit of leaf mass (Williams et al. 1989, Sobrado 1991). In contrast, area-based maximum photosynthetic rates of the three species were not related to leaf lifespan, which is contrary to one of the predictions of the cost-benefit model of leaf lifespans (Kikuzawa 1991). *Cordia*, with intermediate leaf lifespan, but highest foliar N concentrations, had the highest area-based maximum photosynthetic rates. This is in accordance with the pattern of the photosynthesis-foliar N relationship described by Field and Mooney (1986) for a broad range of species.

Photosynthesis of all three species declined with leaf age. The decline was steepest in the case of *Cedrela* and most gradual in the case of *Hyeronima*. This is consistent with a prediction of a cost-benefit model of leaf lifespans (Kikuzawa 1991), and with results suggesting that rate of decline in photosynthesis with leaf age is inversely related to leaf longevity (Kitajima et al. 1997).

Average daily carbon gain calculated using light response curves and PAR data (292-391 mmol m^{-2} d^{-1} for young leaves of the three species) were comparable to the highest values obtained by direct measurement of 24 hr carbon gain by *Ceiba,* another fast-growing tropical tree (370 mmol m^{-2} d^{-1}, although *Ceiba* had higher rates of maximum photosynthesis; Zotz and Winter 1993). Average values of carbon gain calculated for the study species are higher than average values measured by Zotz and Winter (1993) because my calculations are based on PAR measured in June, when insolation is higher than at other times during the year at this latitude, and because the PAR data were for unusually clear days (Figure 3-5 [d]): average daily photon flux density based on the PAR data I used was 42.9 mol m^{-2} d^{-1}, which is close to the maximum values measured at La Selva over a 65 d period from March to November (6.9 to 46.1 mol m^{-2} d^{-1}; Oberbauer et al.1989). Furthermore, my calculations of average daily carbon gain do not take into account mid-day depression in photosynthesis due to stomatal limitation. Mid-day stomatal closure was measured for at least one (*Hyeronima*) of the three study species by Bigelow (1998).

Foliar nutrient contents of the study species were high in comparison with other tropical species. Foliar N concentrations (2.8-4.1%) were almost twice the concentrations reported for a range of tropical forest types (0.7-2.1 %, Medina 1984; 0.9-2.5%, Vitousek

and Sanford 1986). Similarly, foliar P concentrations (0.20-0.34 %) were more than twice the concentrations found in a range of several different tropical forests (0.05-0.16 %, Medina 1984; 0.04-0.14%, Vitousek and Sanford 1986). This almost two-fold difference in foliar nutrient concentrations in comparison with other studies is partially explained by the fact that these concentrations were determined on leaf lamina disks, rather than on whole leaves. Nevertheless, whole-leaf nutrient concentrations for these species (1.9-2.6% N and 0.17-0.27% P; chapter 4) were still fairly high compared to concentrations reported from other studies, and this can be attributed to the nutrient-rich soils of the study site (Chapter 2).

Potential Photosynthetic Nutrient Use Efficiency

Potential PNUE (in μmol CO_2 $[mol\ N]^{-1}\ s^{-1}$) ranged from about 40 to 60. These values are comparable to potential PNUE measured for tropical deciduous species with leaf lifespans of 6-10 months (50-80), and higher than values reported for tropical evergreen species with leaf lifespans of 11-12 months (25-30; Sobrado 1991). In relation to values of potential PNUE reported for tropical early successional species (about 61-144; Ellsworth and Reich 1996), potential PNUE of the study species was quite low. Potential PNUE calculated using nutrient concentrations determined on leaf lamina disks (this study) are lower than calculations using nutrient concentrations determined on whole leaves that include fibrous vein tissue (other studies). For example, potential PNUE calculated using whole-leaf N concentrations (Chapter 4), yields values of 64, 60, and 102 for *Hyeronima*, *Cordia*, and *Cedrela*, respectively, which is more comparable to values reported for other fast-growing, early successional species (Ellsworth and Reich 1996).

Potential PNUE with respect to P was invariant among the study species. Potential PNUE with respect to P measured for a range of deciduous and evergreen species (DeLucia and Schlesinger 1995) also showed very little interspecific variation, which is similar to the results from this study.

Cumulative Photosynthetic Nutrient Use Efficiency

Cumulative PNUE, with respect to both N and P, varied two-fold among species. Differences in cumulative PNUE were strongly influenced by leaf lifespan: *Hyeronima*, with the longest-lived leaves also had the highest cumulative PNUE. Nevertheless, cumulative PNUE of *Cordia* did not differ from that of *Cedrela* even though its leaves were twice as long-lived as those of *Cedrela*.

These findings are consistent with Small's (1972) calculations of a closely related index, "potential photosynthate," for a suite of temperate-zone bog and non-bog evergreen and deciduous species. He found that bog evergreen species, with leaf longevities of 2-3 seasons, had a potential carbon gain per unit of N that was about 200 percent greater than that of non-bog deciduous species, whose leaves lived for only a single season. This is analogous to the difference in cumulative PNUE between *Hyeronima*—with its much longer lived leaves—and the other two species. Furthermore, in comparisons of only the deciduous species from the bog and non-bog habitats, Small (1972) found that the bog species resorbed a larger fraction of N preceding leaf abscission than non-bog species. Thus, even though both had leaves that only lived a single season, the bog species had a potential carbon gain per unit of N that was about 60 percent greater than the non-bog species, by virtue of their differences in resorption alone. This is analogous to cumulative PNUE measured for *Cedrela* and *Cordia*, where the greater

nutrient resorption and higher photosynthesis per unit of nutrient in leaves of *Cedrela* compensates for any difference in cumulative PNUE that would be expected solely on the basis of the greater leaf longevity of *Cordia*.

Ecological Implications

Is it possible to make inferences regarding species' nutrient requirements and competitive abilities in different environments, based on potential and cumulative nutrient use efficiencies? The numerator of the expression for cumulative PNUE (equation 2) can be denoted as the product of average daily carbon gain and leaf lifespan:

$$Cumulative\ PNUE = \frac{\int_{0}^{Lifespan} P_S}{L_N\,(1-Resorption)} = \frac{P_S^{*} \cdot Lifespan}{L_N\,(1-Resorption)} \qquad (6)$$

Rearranging equation 6 yields a product of two terms, a) the ratio of average daily carbon gain to foliar nutrient content, and b) the ratio of leaf lifespan to fraction of foliar nutrients lost at the time of leaf abscission. Furthermore, the ratio of average daily carbon gain to foliar nutrient content is proportional to potential PNUE (equation 1), given that there is a linear relationship between average daily carbon gain and potential maximum photosynthesis (Zotz and Winter 1993). Thus, cumulative PNUE is a function of potential PNUE plus a term that describes the length of time that nutrients are retained by the plant:

$$\frac{P_S^{*} \cdot Lifespan}{L_N\,(1-Resorption)} = \frac{P_S^{*}}{L_N}\,\frac{Lifespan}{(1-Resorption)} \approx Potential\ PNUE\ \frac{Lifespan}{(1-Resorption)} \qquad (7)$$

A high cumulative PNUE can be achieved by a high potential PNUE, or by longer nutrient retention times, or by some combination of the two (equation 7). Reich et al. (1991) suggested that there are trade-offs between having leaves with high photosynthetic rates and leaves that are long-lived. Likewise, there may be tradeoffs between high potential PNUE and longer nutrient retention times: on the one hand, potential PNUE is likely to be higher in short-lived leaves, where photosynthetic tissue is not diluted by carbon-rich protective tissue, and nutrients are less likely to be allocated to non-photosynthetic functions (Field and Mooney 1986); on the other hand, nutrient retention times increase as leaf longevity increases (Escudero et al. 1992). The suggestion of a tradeoff in selection for the components of nutrient use efficiency at the leaf level is analogous to Berendse and Aerts' (1987) proposal of a tradeoff in selection for the components of nutrient use efficiency at the plant level.

The possible tradeoffs between high potential PNUE and longer nutrient retention times are exemplified by two of the three species in this study, *Cedrela* and *Hyeronima,* and provide partial support for the original prediction that high potential PNUE would be associated with short leaf lifespans, whereas high cumulative PNUE would be associated with long-lived leaves (Chapter 1). The species with the shortest-lived leaves, *Cedrela*, has the highest potential PNUE (for N), and is likely to be more successful in environments where nutrient availability is less constraining. The species with the longest-lived leaves, *Hyeronima*, has the highest cumulative PNUE (for N and P) and, of the two, is likely to fare better in environments where nutrients are more limiting. These PNUE-based predictions are supported by the species' natural distribution. *Cedrela* tends to occur in forests on fertile soils, for example along rivers. *Hyeronima*, although it also

occurs on fertile soils, persists in closed forests in environments that are likely to be more competitive (Clark and Clark 1992).

The third species, *Cordia*, has neither high potential PNUE nor high cumulative PNUE, although it has the highest foliar nutrient content and photosynthetic rate of the three species. *Cordia*, therefore, is likely to have the highest productivity of the three species, provided nutrients are amply available. This was observed during the first year following planting of the three species (Haggar and Ewel 1995). By the same token, it follows that *Cordia* would be the first of the three species to experience nutrient deficiency and the effects of belowground competition for resources, and this too has proven to be the case (Haggar and Ewel 1997). These observations are supported by other observations of the species' behavior: *Cordia* readily colonizes old fields on fertile soils, but grows only slowly where planted on less fertile soils (Butterfield 1994).

Given the trade-offs between potential PNUE and nutrient retention, therefore, there are multiple routes to high carbon assimilation per unit of nutrients invested. One way is by having high potential PNUE, provided rapid leaf and nutrient turnover do not jeopardize nutrient availability. This is likely to impart a competitive advantage to species in fertile, high-light environments, where growing larger and faster is the key to resource capture and there is no likely added benefit to be derived from a conservative use of resources.

Although most studies of leaf nutrient use efficiency have focused on potential PNUE, this term explains only part of the story. The other way that high carbon assimilation per unit of foliar nutrient can be achieved is by having low potential PNUE, but greater leaf longevity. Longer lived leaves imply the potential for greater cumulative

carbon gain as well as longer nutrient retention in foliage. This is likely to impart a competitive advantage to species in resource-poor environments, where nutrient conservation, not rapid growth, is the key to persistence and perhaps fitness.

In addition to its implication for species' distributions in natural systems, differences in leaf nutrient use efficiency also have implications for human-managed systems. Fast-growing, high-yielding crops are likely to have higher potential PNUE but rapid leaf and nutrient turnover, consequently higher nutrient requirements, than low-yielding perennials. Species that have high potential PNUE and can avail themselves of high nutrient and light availability, thereby growing bigger faster, may be the species that make good overstories in agroforestry systems. The resources "wasted" by these species, by virtue of their rapid tissue and nutrient turnover, can be utilized by species with longer-lived leaves (e.g., coffee, tea, cacao) that grow slowly, but can persist in the shaded understory. Furthermore, on inherently infertile soils and on degraded landscapes, species with long-lived leaves and longer nutrient retention times are likely the species that will establish and grow—even if only slowly—and so be the most appropriate tools for restoration.

Table 3-1. Specific leaf mass (SLM) and mass- and area-based photosynthetic rates, nitrogen concentrations and phosphorus concentrations for the three species. Photosynthetic rates were interpolated from A-C_i curves at an internal CO_2 concentration of 240 ppm. Values are means (standard errors) of two blocks, each comprising measurements on 10 leaves. (Different letters indicate significant differences at $p < 0.05$).

Species	SLM	Photosynthesis		N Concentration		P Concentration	
	g / m^2	$\mu mol\ m^{-2}\ s^{-1}$	$nmol\ g^{-1}\ s^{-1}$	$mmol / m^2$	% (w/w)	$mmol / m^2$	% (w/w)
Hyeronima	79.85 [ab]	7.88 [a]	99.03 [b]	164.0 [b]	2.8 [b]	5.2 [a]	0.20 [b]
	(4.5)	(0.05)	(5.0)	(9.3)	(0.0)	(0.5)	(0.01)
Cedrela	56.60 [b]	9.51 [a]	167.72 [a]	150.2 [b]	3.7 [a]	6.1 [a]	0.34 [a]
	(5.7)	(1.34)	(7.2)	(23.5)	(0.2)	(0.2)	(0.02)
Cordia	92.26 [a]	10.89 [a]	117.57 [b]	268.8 [a]	4.1 [a]	7.3 [a]	0.25 [b]
	(6.3)	(0.59)	(1.0)	(10.1)	(0.1)	(0.8)	(0.01)

Table 3-2. Leaf lifespan, average daily carbon gain by young and old leaves, and calculation of cumulative carbon gain over leaf lifespans for the three species. Age of old leaves (C) was calculated using leaf position on branches as surrogates for leaf age, assuming that leaves are produced at a constant rate; rate of decline in daily carbon gain (F) was calculated assuming a linear decline in photosynthetic capacity over leaf lifetimes. (See equations 4 and 5 in text.)

Species	(A) Leaf Lifespan	(B) Fraction of Lifespan (old leaves)	(C) Age of Old Leaves [A*B]	Average Daily C Gain		(F) Rate of Decline in Daily C Gain [(E-D)/C]	(G) Cumulative C gain [½ * F *A^2 + D*A]
				(D) young	(E) old		
	(d)		(d)	(mmol m^{-2} d^{-1})		(mmol m^{-2} d^{-2})	(mol / m^2)
Hyeronima	176	0.61	107.4	292.2	189.6	-0.96	36.6
Cedrela	50	0.68	34.0	353.9	303.1	-1.49	15.8
Cordia	99	0.71	70.3	391.7	314.0	-1.11	33.4

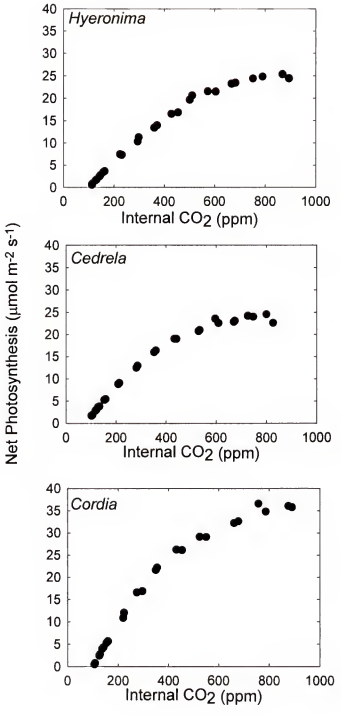

Figure 3-1. Response of photosynthesis to changing internal CO_2 concentration. Sample curves for the three species.

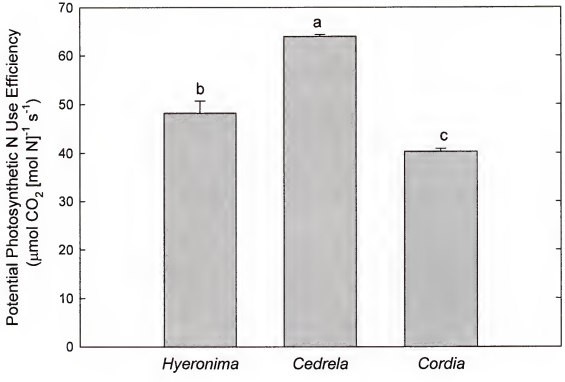

Figure 3-2. Instantaneous photosynthetic N use efficiency. Values are means (standard errors) of two blocks, each comprising measurements on 10 leaves.

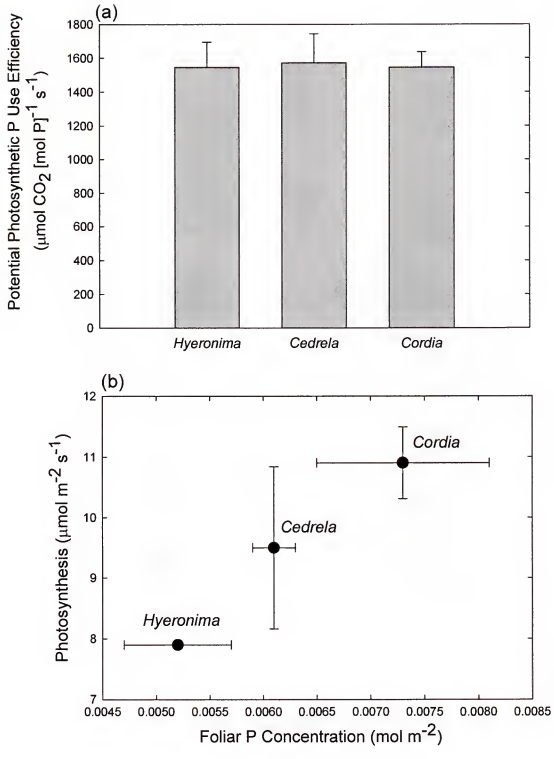

Figure 3-3. (a) Instantaneous photosynthetic P use efficiency. (b) Net photosynthesis as a function of foliar phosphorus concentration. All values are means (standard errors) of two blocks, each comprising measurements on 10 leaves.

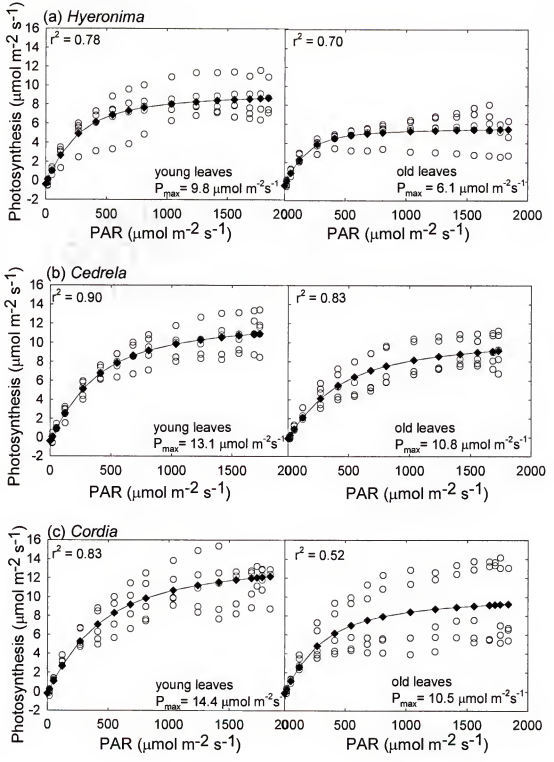

Figure 3-4. The response of photosynthesis to changing light for five young and five old leaves of (a) *Hyeronima*, (b) *Cedrela*, and (c) *Cordia*. The solid lines denote non-rectangular hyperbolas fitted to the data.

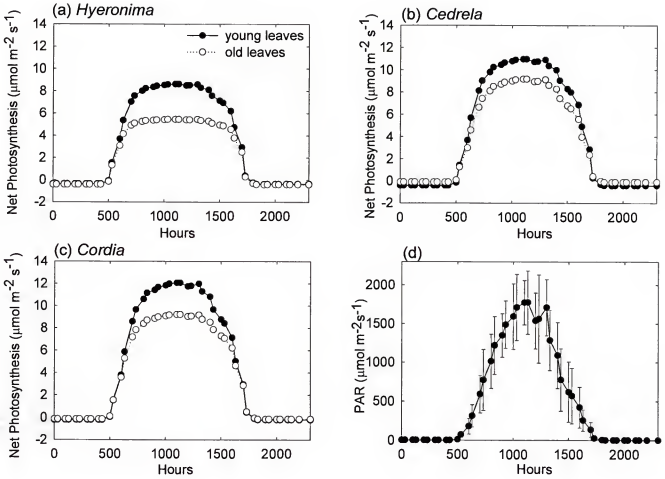

Figure 3-5. Daily course of net photosynthesis for young and old leaves of (a) *Hyeronima*, (b) *Cedrela*, and (c) *Cordia*. Daily photosynthesis was calculated using (d) average PAR measured for 6 consecutive days in June 1995.

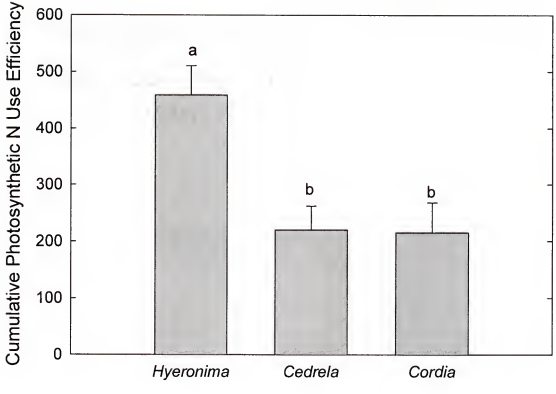

Figure 3-6. Cumulative phostosynthetic N use efficiency (mol m^{-2} CO_2 [mol m^{-2} $N]^{-1}$). Values are means (standard error) of two blocks.

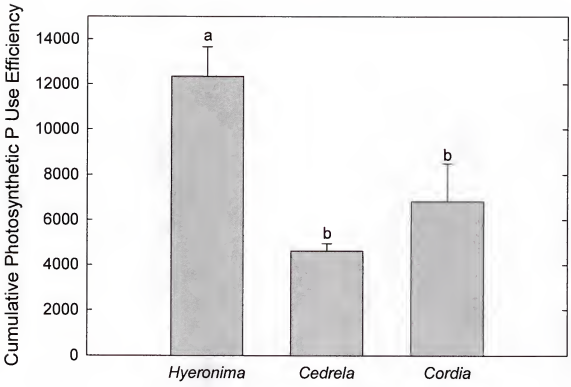

Figure 3-7. Cumulative phostosynthetic P use efficiency (mol m^{-2} CO_2 [mol m^{-2} P]$^{-1}$). Values are means (standard error) of two blocks.

CHAPTER 4
NUTRIENT USE EFFICIENCY AT THE PLANT LEVEL

Introduction

The area under plantations in the tropics has more than trebled since the early 1980s (Brown et al. 1997). The purposes for which these plantations are established range from timber production, to agroforestry, to restoration of degraded and abandoned lands for soil and water conservation. These plantations, despite their diverse nature, share certain constraints—they are often consigned to soils that are either inherently infertile or have been greatly impoverished due to previous land-use practices, and more often than not, large fertilizer subsidies are not an economically viable option in their management (Brown et al. 1997). Given these limitations to their management, there are several objectives that need to be considered: one is to achieve productivity under potentially infertile conditions in the short term; the other is to sustain productivity and soil fertility in the long term.

Nutrient use efficiency—the efficiency with which plants utilize nutrients that they obtain from the soil for biomass production—is relevant to the issues of productivity and soil fertility; it should, therefore, be an important criterion in species selection for reforestation and restoration. Plant nutrient use efficiency is the ratio of total biomass produced to total nutrients taken up (Hirose 1975). This ratio is a measure of physiological and ecological functioning that integrates processes across scales ranging

from photosynthesis at the level of individual leaves, to nutrient cycling between plant and soil.

Plant nutrient use efficiency depends on total nutrient uptake, and on the efficiency with which nutrients taken up are used for biomass production. Total uptake, in turn, is a function of a plant's root morphology and physiology, and also depends on the degree to which nutrients are conserved in the plant. A plant that internally recycles a large proportion of its nutrients through resorption prior to leaf abscission needs to take up less nutrients from the soil to meet its nutrient requirements, whereas a plant that loses large quantities of nutrients in litterfall or leaching from the crown needs to take up more nutrients from the soil to replenish these losses.

Comparisons of communities along gradients of soil fertility show that communities in less fertile environments have a higher efficiency in their use of nutrients as evidenced by less nutrient return to soil in litterfall (Vitousek 1982, 1984, Cuevas and Medina 1986, Silver 1994). By the same token, it has been suggested that evergreens have a higher efficiency of nutrient use than deciduous species, due to greater longevity of foliage and less tissue and nutrient turnover (Monk 1966, Schlesinger et al. 1989, Cole and Rapp 1981, Waring and Schlesinger 1985, Aerts 1995), although being evergreen does not necessarily imply greater leaf longevity (Kikuzawa 1991). Despite the widely held view that high nutrient use efficiency is a characteristic of species in low-nutrient environments, there is also some evidence for the opposite phenomenon, namely that nutrient use efficiency may actually be greater under conditions of higher nutrient availability. For example, when fertilized, certain species demonstrate greater nutrient resorption from leaves prior to abscission (Nambiar and Fife 1991, Chapin and Moilanen

1993, Lennon et al. 1985). In addition, as suggested by Grubb (1989), plants in low fertility environments may allocate proportionally more biomass to leaf tissue (Grubb 1977), leading to a lower nutrient use efficiency of the plant as a whole, due to the greater nutrient costs of producing leaf biomass compared to wood.

I examined plant nutrient use efficiency with respect to nitrogen (N) and phosphorus (P) in relation to productivity, nutrient uptake, and internal recycling of nutrients in three species of fast-growing tropical trees. The three species, *Hyeronima alchorneoides*, *Cedrela odorata*, and *Cordia alliodora* were grown under uniform conditions at La Selva Biological Station in Costa Rica (Chapter 2). The warm, moist conditions at the site are conducive to rapid, year-round growth, providing an opportunity to study nutrient use efficiency at the plant level in large-statured trees. Although the site is on fertile soil, P is likely to be relatively more limiting to plant productivity than N, given the soil's volcanic origin and the potential for P fixation by the soil. Thus I hypothesized first, that the species would show marked differences in nutrient use efficiency with respect to P, but not with respect to N. Furthermore, the species represent a range of biomass allocation patterns and leaf characteristics (Haggar and Ewel 1995). *Hyeronima* has the longest lived leaves of the three species, followed by *Cordia* and then *Cedrela* (Chapter 3). Given the proposed relationship between leaf longevity and nutrient conservation by plants, I further hypothesized that nutrient use efficiency at the whole plant level by the three species would follow the pattern *Hyeronima* > *Cordia* > *Cedrela*.

Methods

Nutrient use efficiency was estimated for June 1995-June 1996. Plant nutrient use efficiency is denoted as follows:

$$Plant\ NUE = \frac{NPP}{Total\ Nutrient\ Uptake}$$

where NPP is aboveground net primary productivity of an individual, and total nutrient uptake includes nutrients accrued in standing aboveground biomass as well as nutrients taken up but subsequently lost in litter or by leaching from the crown.

Productivity

Aboveground NPP from mid-1995 to mid-1996 was calculated as the algebraic sum of the change in biomass, and total litter. Biomass of tissues (stems, branches, petioles or rachises, and leaves) was determined using allometric equations relating biomass to tree height and diameter (Satoo and Madgwick 1982). Starting in 1991, a total of 24 individuals of each species were harvested annually from zones designated for destructive sampling in the study plots. (The number of harvested individuals was reduced to 18 in 1993, and 6 in 1996). Harvested trees were separated into stems, branches, petioles (or rachises), and leaves. Fresh mass of each biomass component was determined in the field, and a subsample was dried to constant weight at 70 °C and weighed to obtain dry mass.

The best fits of the relationship between biomass and plant size were obtained using equations of the form $\log W = \log a + b \log (X)$, where W is biomass of the component being assessed (stems, leaves, branches, and petioles or rachises) and X is a

compound measured of plant size (either HD^2, or HD; H = height, and D = diameter). The r^2-values obtained were between 0.47-0.94. Equations were modified as larger individuals were added to the data set each year. Inventories of tree heights and diameters in June 1995 and June 1996 provided the input to the allometric equations. Litter was collected biweekly from three 1.73 x 0.50 m traps in each plot, then dried at 70 °C and weighed. Average litter produced per tree was calculated by dividing total litter per unit area by the number of individuals per unit area.

Nutrient Uptake

Nutrient uptake was estimated as the sum of net nutrient uptake and nutrients lost in litterfall and foliar leaching. Net uptake of N and P was calculated by summing the products of nutrient concentrations in leaves, stems, branches, and petioles or rachises, times the change in biomass of each fraction. Nutrient concentrations were determined on tissue subsamples of individuals harvested annually to provide data for the allometric equations. Tissue samples were dried at 70 °C, ground to pass a 2 mm sieve and analyzed for total N and P (Tabatabai and Bremmer 1991).

Nutrients lost in litter were calculated by multiplying foliar nutrient concentration by the fraction of nutrients not resorbed prior to leaf abscission. Nutrient resorption was measured in July-August 1995. Resorption was estimated as the difference between nutrient concentrations of living and recently abscised leaves, expressed as a proportion of the nutrient concentration of living foliage. Resorption was estimated on a leaf area basis, because leaf area is conserved whereas leaf mass can change over a leaf's lifetime, due to resorption of carbon (in addition to nutrients) prior to abscission (Chapin and Van Cleve 1989). Living, sun-lit foliage was sampled from five trees per plot using a pole

pruner. Because young, apparently fully expanded leaves may not have attained peak foliar nutrient concentrations (Bigelow 1992), leaf position was treated as a surrogate for leaf age, and samples were restricted to three mature leaves per branch immediately distal to the youngest, fully expanded leaf. Fresh litter was collected daily over a 3 wk period in three 1 x 1 m suspended net traps in every plot. Daily collections were made to avoid nutrient leaching by rainfall, as is likely if litter remains in traps for extended periods of time (Chapin and Van Cleve 1989). Nutrient concentrations were measured on inter-vein lamina disks, 0.25 cm^2 in diameter, punched out of living and abscised leaves (Medina 1984). Disks were dried and digested following a modified Kjeldahl procedure; N and P were analyzed on a Technicon Autoanalyzer by the salicylate/nitroprusside and the antimony/molybdate methods, respectively (Technicon 1973).

Foliar leaching losses were calculated by multiplying net concentrations of nitrate (NO_3-N), ammonium (NH_4-N) and P (PO_4-P) in samples of stemflow and throughfall water by estimates of total annual volumes of stemflow and throughfall. Net concentrations of NO_3-N, NH_4-N and PO_4-P were obtained by subtracting concentrations in rainwater from concentrations in stemflow and throughfall water. Spiral stemflow collars were placed on 18 individuals of each species. Sampling of individuals was stratified so that six trees were selected at random in each of the three experimental blocks. Epiphytes were removed from a 30 cm band around the trunk at a height of about 150-180 cm from the ground before affixing collars to the trees. Collars were constructed either from strips of rubber foam or rubber gasket. An acetate strip glued to the outer wall formed a channel between 2 and 2.5 cm wide. The trunk and collar junction was sealed with silicone caulk. Each stemflow collar was connected to two collectors in series. The

first collector was a 125 ml nalgene bottle placed immediately below the collar, well above any possible contamination by splashing from the soil, and held in place by an elastic band around the trunk. This, in turn, was connected to a 20 l plastic container through an overflow spout in its cap. The nalgene bottles were used to collect clean stemflow samples for chemical analysis; the bottles were replaced with clean, acid-washed bottles after each collection. The 20 l containers were used to collect samples for volume determination. Stemflow volumes were measured to the nearest 5 ml. Volumes were measured on an event-by-event basis for 27 separate precipitation events ranging from 0.25 to 55.80 mm. If there was a rain-free gap of more than an hour during a rainfall event, it was treated as two events. Rainfall depths corresponding to stemflow events were measured with an automatic tipping-bucket raingauge, calibrated to measure a minimum rainfall of 0.254 mm. Samples for stemflow chemistry were obtained for 12 rain events ranging from 0.49 to 33.07 mm. To avoid possible contamination by algal growth in the stemflow collars, collars were scrubbed weekly and rinsed with deionized water. Samples of rainwater corresponding to stemflow collection were obtained using a 20 cm diameter funnel mounted in an adjacent clearing. The entire apparatus was dismantled weekly and scrubbed.

Throughfall volume data used were those of Casey (1996). He collected throughfall in five 2 m long by 0.05 m wide trough gauges per plot, in one block of the experiment. The troughs were placed 30 cm above the soil, and slanted to channel throughfall into covered plastic buckets. Corresponding rainfall depth was measured using twelve 15 cm diameter funnels located in a clearing outside the plots. Throughfall was measured for 34 rain events ranging from 0.02 to 5.94 mm. Samples for throughfall

chemistry were collected by me in five 15 cm diameter funnels per plot, in one block of the experiment. The funnels were elevated 1 m above the ground to avoid contamination by splashing. Funnels were connected to 125 ml nalgene bottles. A glass wool plug was placed in each funnel to trap debris that might contaminate the sample. Samples were collected for eight rain events ranging from 0.49 to 33.07 mm. After each collection the nalgene bottle was replaced by an acid-washed bottle, the funnel was rinsed with deionized water, and the glass wool plug was changed.

Samples for stemflow and throughfall chemistry were filtered through a 0.45 μ glass fiber filter (Gelman Sciences Type A/E), fumigated with a drop of chloroform, and frozen until analysis. Samples were analyzed for PO_4-P following a modified antimony/molybdate protocol (Murphy and Riley 1962) on a spectrophotometer. NO_3-N and NH_4-N were analyzed on an Alpkem Autoanalyzer using standard procedures (Alpkem 1986).

Statistical Analysis

To develop equations for stemflow and throughfall volume as a function of rainfall amount, linear regression models were fitted to the stemflow and throughfall volume data subsequent to log-transformation. Analyses were performed using the REG procedure in SAS (SAS Institute 1988).

Differences in net primary productivity, nutrient uptake and nutrient use efficiency were analyzed using a one-way analysis of variance with species as the main effect. Interspecific differences in mean productivity, uptake, and nutrient use efficiency were tested using contrasts within the analysis of variance. Analyses were done with the

GLM procedure in SAS (SAS Institute 1988). Post-hoc tests for power of the analyses of variance were performed using JMP (SAS Institute 1996).

Results

Aboveground NPP

Aboveground NPP per individual for these 4.5 yr old trees ranged from about 5 kg/yr for *Cordia* to about 14.5 kg/yr for *Hyeronima* (Table 4-1). At the tree spacing used, this is equivalent to aboveground NPP of 9 to 23 Mg ha^{-1} yr^{-1}. Of the three species, *Hyeronima* allocated the greatest proportion of aboveground standing biomass to leaves (about 9%) followed closely by *Cordia* (8%), whereas *Cedrela* allocated only about 6% of aboveground standing biomass to leaves. Leaf turnover rates, calculated on the basis of standing biomass of leaves and annual litterfall, were highest for *Cedrela* (2.7 yr^{-1}) followed by *Cordia* (2.2 yr^{-1}) and then *Hyeronima* (1.5 yr^{-1}). This correlates with leaf lifespans measured by direct tagging of leaves (about 50, 99 and 176 d for *Cedrela*, *Cordia*, and *Hyeronima*, respectively; Chapter 3), although estimates of lifespans based on leaf turnover rates (equivalent to about 134, 168 and 245 d for *Cedrela*, *Cordia*, and *Hyeronima*, respectively) were greater than measured leaf lifespans.

Nutrient Uptake

Tissue concentrations of N and P tended to be highest in *Cordia* and lowest in *Hyeronima* (Table 4-2). Litter nutrient concentrations were estimated as the fraction of foliar nutrients not resorbed prior to leaf abscission, after adjusting for changes in specific leaf mass accompanying leaf abscission. Mean resorption of nutrients was greater by *Hyeronima* and *Cedrela* (about 50% and 44% for N and P, respectively) than by *Cordia*

(37% and 18% for N and P, respectively), although these differences were not significant due to the larger variances associated with leaf nutrient concentrations in *Cordia* (Figure 4-1). Concentrations of N and P in *Cordia* litter tended to be higher than in *Hyeronima* and *Cedrela* litter, as a consequence of its higher foliar nutrient concentrations and lower nutrient resorption.

Concentrations of NO_3-N, NH_4-N, and PO_4-P in stemflow and throughfall were extremely low, ranging from a few tenths of a mg/l to a few mg/l (Figure 4-2). Concentrations of NH_4-N and PO_4-P in stemflow and throughfall were elevated relative to concentrations in rainwater, indicating leaching of these ions. Average NO_3-N concentrations in stemflow and throughfall were, in contrast, lower than in rainwater, suggesting that NO_3-N is retained in the crown (Table 4-3). Nutrient concentrations in stemflow collected during smaller rain events (< 10 mm for NO_3-N, NH_4-N, and < 16 mm for PO_4-P) tended to be higher than in water collected during larger rain events, although concentrations were extremely variable from event to event, and from species to species (Figure 4-2 a). Nutrient concentrations in throughfall were only weakly related to event size (Figure 4-2 b), although this could be due to the smaller number of events sampled.

The species varied in stemflow and throughfall traits, as indicated by the different slopes of the regressions of stemflow and throughfall against rainfall (Table 4-4). *Hyeronima* funneled a greater proportion of total rainfall as stemflow (about 2 %) than either *Cedrela* (about 0.3 %) or *Cordia* (about 0.7 %). Throughfall, on the other hand, constituted a smaller proportion of total rainfall for *Hyeronima* (about 59 %) compared to the other two species (about 86 and 79 % for *Cedrela* and *Cordia*, respectively). As a result, the proportion of total rainfall reaching the ground in stands of *Hyeronima* (61%)

was less than in stands of the other two species (86.3% and 79.7% for *Cedrela* and *Cordia*, respectively). The difference in relative volumes of throughfall and stemflow associated with the three species can be attributed to their different crown architectures—*Hyeronima*, with plagiotropic branches and high leaf area index, has a denser crown than either the orthotropically branched *Cedrela* with low leaf area index, or the open, tiered crown of *Cordia* (Menalled 1996).

The best relationship between throughfall and rainfall depth was a simple linear regression of the log-transformed data. For stemflow volume as a function of rainfall depth—in the case of *Hyeronima* and *Cordia*—the best fit for the data was obtained using a multiple regression model that included log-transformed stem diameter^2 as a second, independent variable. This is analogous to treating diameter^2 as a covariate. For *Cedrela*, diameter^2 was not a significant effect in the model, and a simple regression with log-transformed rainfall as the only independent variable provided the best fit for the data. Stemflow data were inherently more variable than throughfall data, as indicated by the substantially lower r^2-values obtained for the stemflow equations, compared to the throughfall equations (Table 4-4).

The magnitudes of total nutrients leached varied as much as six-fold across species (Table 4-5), primarily as a result of differences in volumes of stemflow and throughfall. *Hyeronima*, the species that funneled the largest amounts of water as stemflow, also had the highest stemflow losses of NH_4-N and PO_4-P. Throughfall losses of NH_4-N were more similar among species, but throughfall losses of PO_4-P were highest from *Hyeronima*. Overall, stemflow and throughfall constituted only a minor pathway for

losses of N, whereas the amount of P lost via leaching from the crown was a substantial proportion of total P losses.

Hyeronima had the greatest total N uptake of the three species (Figure 4-3). A surprisingly large fraction of total N taken up was lost in litterfall by all three species: *Hyeronima* shed about half its total N uptake; *Cedrela* and *Cordia,* in comparison, lost more than two-thirds of total N taken up. Loss of N via leaching by stemflow and throughfall was a negligible proportion of total uptake.

Total P uptake did not differ significantly among species (Figure 4-4). For *Cordia*, about a third of total P taken up was lost in litterfall; for *Cedrela* and *Hyeronima*, on the other hand, only about one fourth of total P taken up was lost in litterfall. Leaching of P from the crowns constituted a considerable fraction of total uptake, and ranged from about 4 to12%.

Nutrient Use Efficiency

N use efficiency of the three species did not differ significantly ($p = 0.44$). Nevertheless, there was an almost twofold difference in N use efficiency between *Hyeronima*, the species with the highest N use efficiency, and *Cordia,* the species with the lowest N use efficiency (Figure 4-5). The inability to detect a significant effect of species on N use efficiency can be attributed to the very low power (a 75% probability of failing to reject a false null hypothesis) of the test, given the small number of replicates ($n = 3$).

P use efficiency by *Hyeronima* was greater than that of the other two species ($p < 0.05$; Figure 4-6). The pattern of P use efficiency by the three species mirrored their

pattern of biomass production, since there were no differences in P uptake by the three species.

Discussion

Aboveground NPP and Nutrient Uptake

Aboveground NPP of the three species at age 4.5 yr ranged from about 9 to 23 Mg ha^{-1} yr^{-1}. These values are toward the high end of the range compared with other fast-growing tropical species. For example, Lugo et al. (1988) reported aboveground NPP between 1.6 and 29.8 Mg ha^{-1} yr^{-1}, with a median value of about 12 Mg ha^{-1} yr^{-1}, for a number of plantation species from across the tropics.

At age 4 yr, nutrient standing stocks of these species were 194-248 kg/ha N and 30-46 kg/ha P. Surpisingly, these values are lower than those (180-410 kg/ha N, 50-80 kg/ha P) reported by Montagnini and Sancho (1994) for native trees of different species but of the same age grown on less fertile soils close to the site. The differences are due to higher nutrient concentrations (but not biomass) measured by Montagnini and Sancho (1994).

Nutrient uptake is the sum of nutrient accrual and nutrient losses via litterfall and leaching from the crown. Losses of nutrients in litterfall are determined by rates of tissue turnover and the proportion of nutrients resorbed prior to abscission. Of the three species, *Hyeronima* and *Cedrela* showed fairly high resorption of both N (about 55%) and P (about 40%) prior to leaf abscission, while resorption by *Cordia* tended to be somewhat lower. Across a broad spectrum of species and biomes average proportions of foliar nutrients resorbed range from 40 to 60 % (Chapin and Kedrowski 1983, Medina 1984),

although foliar nutrient resorptions of up to 80% (by some mangrove species; Lugo 1998) and even 90% (species of larch; Gower and Richards 1990) have been reported.

Losses of N via leaching from the crowns of the species studied were fairly small. Other studies have estimated annual N leaching losses of the order of 5.0 (Hölscher et al. 1998) to 6.9 kg/ha (with a range of 0.5 to 22.1 kg/ha; Cole and Rapp 1981), whereas I estimated annual N losses of only about 0.1 to 0.5 kg/ha. My estimates of annual P leaching losses, on the other hand, were higher than reported elsewhere: 1 to 3 kg/ha, compared with 0.5 (with a range of 0.1 to 1.9 kg/ha; Cole and Rapp 1981) to 0.8 kg/ha (Hölscher et al. 1998).

One reason for the low N leaching losses in this study is that I found reduced concentrations of NO_3-N in stemflow and throughfall water relative to rainwater, suggesting some N retention in the crown. Although NH_4-N is the form of N that is more commonly known to be taken up by foliage (Parker 1983), there is some evidence for both NH_4-N, and NO_3-N retention in crowns (Horn et al. 1989, Potter et al. 1991, Clark et al. 1998). A second reason for the low estimates of N leaching losses may be my failure to measure organic N, which constitutes as much as a third of total incoming N in rainwater at the site (Eklund et al. 1997) and can range from between a third (Eaton et al. 1973) to four times (Manokaran 1980) the amount of inorganic N in stemflow and throughfall. Nevertheless, because N leaching from the crown constitutes such a negligible fraction (< 0.5%) of total N uptake, even a four-fold increase in the estimate of N leaching losses would not substantially alter the calculation of total N uptake, and consequently, of N use efficiency.

Nutrient Use Efficiency

Whole tree nutrient use efficiency of the three species in this study, with respect to both N (88-141) and P (447-947), was fairly low when compared with a number of other fast-growing species (Table 4-6). *Cordia*, in particular, had low N and P use efficiencies relative to other species. *Cedrela* N use efficiency, though low, was still comparable to other species, but *Cedrela* P use efficiency was less than other reported values. *Hyeronima* N and P use efficiencies were within the range of other reported values.

What accounts for the low nutrient use efficiencies of the study species? One possible explanation is the different ways that litter nutrient concentrations are obtained. Infrequently collected litter (as used in most studies) is susceptible to nutrient leaching between collections (Chapin and Van Cleve 1989), so nutrient use efficiency calculations based on leached litter would yield higher values than calculations based on the higher nutrient concentrations of fresh litter. Nevertheless, when I tested this possibility by recalculating nutrient use efficiency using nutrient concentrations in litter collected bi-weekly, the estimates did not change, because nutrient concentrations obtained the two ways were not markedly different. Rapid colonization of litter by decomposer organisms, especially under the warm, humid conditions that prevail at our site, might cause a secondary increase in litter N (Melillo et al. 1982) and P (Ostertag 1998) concentrations that counters initial litter nutrient losses via leaching. Thus, the possibility remains that the use of leached litter values accounts for the higher nutrient use efficiencies reported in other studies, but I lack unequivocal evidence.

Another explanation for the low nutrient use efficiencies measured for the study species is that the soil at the study site is relatively fertile. Values of extractable N and P at the site are high, compared to a range of other humid tropical sites (Chapter 2). Nevertheless, even under the same conditions, there is practically a twofold difference in both N and P use efficiency among the three species. This wide variation in nutrient use efficiency among the species may be explained based on relative differences in their resource use characteristics.

Resource Use Characteristics

Plant nutrient use efficiency depends on total nutrient uptake by a plant, and on the efficiency with which nutrients taken up are used for biomass production. Berendse and Aerts (1987) stated this more formally, proposing that nutrient use efficiency is a product of two components: nutrient productivity, and the mean residence time of nutrients. Nutrient productivity, defined as the ratio of plant biomass increment to total nutrients in the plant (Ågren 1983), depends on the efficiency with which foliar nutrients are used for photosynthesis (Garnier et al. 1995) and on biomass and nutrient allocation to photosynthetic tissue; it is an instantaneous measure of nutrient use efficiency. Mean residence time is a function of tissue longevity and nutrient resorption; it is a measure of nutrient conservation by plants.

Recently, Garnier and Aronson (1998) reviewed the relationship between nutrient use efficiency and its two components, nutrient productivity and mean residence time of nutrients. I applied an analysis similar to theirs to elucidate some of the factors underlying interspecific differences in nutrient use efficiency. Nutrient productivities (in g biomass/g nutrient) of the three species calculated for the 1995-96 measurement period

ranged from 47 to 80 for N and 222 to 425 for P. Mean residence time of nutrients is the ratio of standing stock to the flux (either uptake from the soil, or litter plus crown-leaching losses, in the case of a steady state plant). Although the study species are still accruing woody biomass and are not yet at steady state, leaf area indices of all three species plateaued following canopy closure (at 10, 14, and 16 months for *Cordia*, *Hyeronima*, and *Cedrela*, respectively; Haggar and Ewel 1995). By assuming steady-state leaf mass, I was able to estimate residence times in the canopy for N and P.

Nutrient use efficiency, with respect to both N and P showed only a weak correlation with nutrient productivity and mean residence time of nutrients across species (Figure 4-7). More importantly, when the data are examined this way, it is apparent that the intraspecific differences in nutrient use efficiency are as marked as the interspecific differences in nutrient use efficiency.

The observed differences in nutrient use efficiency within species, between blocks, is related to differences in biomass production (Table 4-1), rather than to differences in tissue nutrient concentration (Table 4-2). Basal area increments over the measurement interval (1995-96) indicate greater growth in one replicate each of *Cedrela* and *Cordia*. These disproportionately large basal area increments are correlated with disproportionately high aboveground NPP in these replicates, consequently higher nutrient use efficiency of individual trees.

Until now, the discussion has treated nutrient use efficiency as a species characteristic subject to bottom-up controls by plant resource use characteristics (nutrient productivity and mean residence time of nutrients). Other investigators have, similarly, related interspecific differences in nutrient use efficiency to leaf-level characteristics,

whether to differences in leaf longevity affecting the length of nutrient retention (Cole and Rapp 1981, Chabot and Hicks 1982, Waring and Schlesinger 1985), or differences in nutrient resorption affecting the degree of internal recycling by plants (Gray 1983, Schlesinger et al. 1989, DeLucia and Schlesinger 1995). Nevertheless, these findings suggest that nutrient use efficiency is controlled, in addition, by larger scale factors such as intraspecific competition. These top-down controls on nutrient use efficiency are explored further in the following chapter on ecosystem level nutrient use efficiency.

Table 4-1. Above ground biomass, litter production and NPP for average individuals of the three species. Values are means of three replicates (with standard errors) in kg/yr.

		Hyeronima	*Cedrela*	*Cordia*
Standing Stock (1995)	Leaves	2.64 (0.17)	1.10 (0.01)	1.38 (0.13)
	Rachises/ Petioles	—	0.45 (0.01)	0.06 (0.01)
	Branches	7.01 (0.16)	3.75 (0.06)	3.12 (0.38)
	Stems	23.96 (0.50)	10.46 (0.13)	11.96 (1.82)
Standing Stock (1996)	Leaves	3.90 (0.18)	1.20 (0.02)	1.48 (0.07)
	Rachises/ Petioles	—	0.44 (0.01)	0.07 (0.01)
	Branches	7.77 (0.12)	5.05 (0.12)	3.16 (0.24)
	Stems	31.55 (0.48)	13.39 (0.29)	14.05 (1.16)
Litter Produced (1995 - 1996)		4.92 (0.14)	3.11 (0.17)	3.04 (0.31)
ANPP (1995 - 1996)		14.53 (0.53)	7.44 (0.58)	5.28 (1.18)

Table 4-2. Tissue concentrations of (a) nitrogen and (b) phosphorus. Values are percent mass, and are means (standard errors) of composite samples from three blocks.

(a) Nitrogen

	Hyeronima		*Cedrela*		*Cordia*	
	1995	1996	1995	1996	1995	1996
Leaves	2.33 (0.06)	1.85 (0.15)	2.79 (0.04)	2.34 (0.12)	3.32 (0.03)	2.59 (0.16)
Petioles/Rachises	†	†	0.97 (0.06)	0.96 (0.03)	1.38 (0.04)	1.42 (0.21)
Branches	0.67 (0.05)	0.45 (0.04)	0.53 (0.04)	0.64 (0.06)	0.73 (0.10)	0.75 (0.02)
Stems	0.19 (0.02)	0.32 (0.04)	0.35 (0.04)	0.35 (0.02)	0.38 (0.04)	0.45 (0.00)
Litter	0.96 (0.08)		1.22 (0.06)		1.29 (0.13)	

Figure 4-2. (Continued)

(b) Phosphorus

	Hyeronima		*Cedrela*		*Cordia*	
	1995	1996	1995	1996	1995	1996
Leaves	0.13 (0.01)	0.17 (0.01)	0.17 (0.01)	0.26 (0.01)	0.20 (0.02)	0.27 (0.01)
Petioles/Rachises	†	†	0.23 (0.01)	0.38 (0.01)	0.23 (0.002)	0.32 (0.05)
Branches	0.11 (0.01)	0.10 (0.01)	0.12 (0.02)	0.17 (0.01)	0.21 (0.02)	0.26 (0.01)
Stems	0.07 (0.01)	0.08 (0.01)	0.07 (0.002)	0.10 (0.01)	0.11 (0.001)	0.14 (0.02)
Litter	0.10 (0.01)		0.15 (0.01)		0.18 (0.01)	

Table 4-3. Concentrations of NO_3-N, NH_4-N and PO_4-P in rain water, stemflow and throughfall. Values are mg/l.

	Rain water	Stemflow			Throughfall		
		Hyeronima	*Cedrela*	*Cordia*	*Hyeronima*	*Cedrela*	*Cordia*
NO_3-N							
mean	0.05	0.01	0.03	0.04	0.01	0.02	0.01
std.dev.	0.05	0.01	0.04	0.06	0.01	0.02	0.01
number of events	12	10	8	10	8	8	8
NH_4-N							
mean	0.10	0.17	0.20	0.40	0.14	0.12	0.11
std.dev.	0.13	0.22	0.27	0.58	0.09	0.09	0.07
number of events	11	10	8	10	8	8	8
PO_4-P							
mean	0.02	0.57	0.95	0.81	0.15	0.04	0.06
std. dev.	0.07	0.51	0.77	0.72	0.18	0.08	0.10
number of events	12	10	8	10	8	8	8

Table 4-4. Equations used to calculate (a) stemflow volume based on event-by-event rainfall data, y = log (stemflow volume), x = log (rainfall depth), z = log (diameter^2) in the case of *Hyeronima* and *Cordia;* and (b) throughfall depth based on event-by-event rainfall data, y = log (throughfall depth), x = log (rainfall depth)

(a)

Species	Model	r^2
Hyeronima	y = -7.3702 + 2.3730 x + 3.1499 z	0.58
Cedrela	y = -0.2752 + 1.8725 x	0.52
Cordia	y = -1.7171 + 2.1547 x + 0.7181 z	0.56

(b)

Species	Model	r^2
Hyeronima	y = 0.7355 x - 0.0064	0.94
Cedrela	y = 0.8878 x - 0.0047	0.98
Cordia	y = 0.8101 x - 0.0027	0.97

Table 4-5. Estimated annual fluxes of (a) nitrogen and (b) phosphorus in stemflow and throughfall. Fluxes of nitrogen and phosphorus in litterfall are included for comparison with fluxes in crown leaching. Values are in mg/individual. (Negative signs indicate losses from the canopy, positive signs indicate apparent retention in the canopy.)

(a)

Species	NO_3-N		NH_4-N		Annual N Losses	
	stemflow	throughfall	stemflow	throughfall	crown leaching	litterfall
Hyeronima	+ 49	+247	- 51	- 493	- 248	-61,300
Cedrela	+ 2	+217	- 9	- 435	- 225	-48,300
Cordia	+ 7	+299	- 44	- 299	- 37	-53,100

(b)

Species	PO_4-P		Annual P Losses	
	stemflow	throughfall	crown leaching	litterfall
Hyeronima	- 769	- 1,232	- 2,001	-4,300
Cedrela	- 50	- 435	- 485	-3,200
Cordia	- 136	- 599	- 735	-3,900

Table 4-6. Whole tree (above-ground) nutrient use efficiency with respect to nitrogen and phosphorus. Included, for comparison, are values of nutrient use efficiency obtained from studies in plantations of fast-growing species from a tropical (Puerto Rico), a sub-tropical (the lower Himalayas), and a temperate (Wisconsin) site using the same methods as used in this study. (Values are g biomass / g nutrient.)

Species	Age (yrs)	Nitrogen Use Efficiency	Phosphorus Use Efficiency	Location	Source
Hyeronima alchorneoides	**4.5**	**141**	**947**	**Costa Rica**	**This study**
Cedrela odorata	**4.5**	**135**	**495**		
Cordia alliodora	**4.5**	**88**	**447**		
Populus deltoides	5.0	160	1379	Lower Himalayas, India	Lodhiyal et al. 1995
Casuarina equisetifolia	5.5	357	1428	Puerto Rico	Wang et al. 1991
Albizia procera	5.5	222	1111		
Eucalyptus robusta	5.5	345	833		
Leucaena leucocephala K8	5.5	128	1111		
Leucaena leucocephala P.R.	5.5	153	1250		
Red oak (*Quercus rubra*)	26.5	320	1800	Wisconsin, USA	Son and Gower 1991
European larch (*Larix decidua)*	26.5	480	3750		
White pine (*Pinus strobus*)	26.5	140	1500		
Red pine (*Pinus resinosa*)	26.5	135	950		
Norway spruce (*Picea abies*)	26.5	135	750		

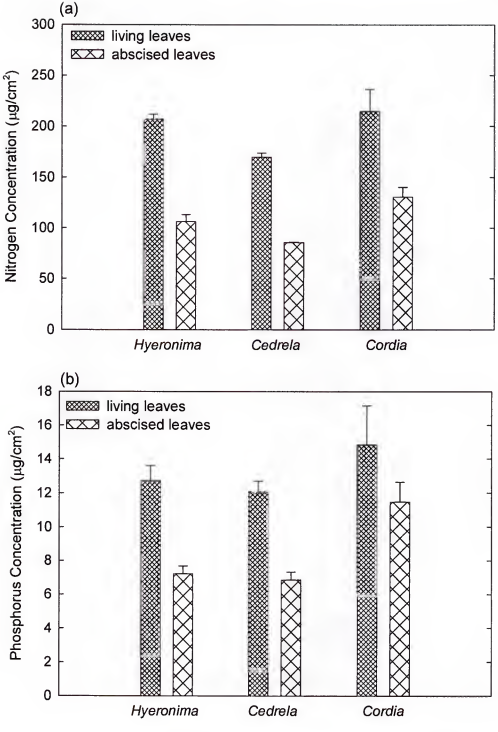

Figure 4-1. Concentrations of (a) nitrogen, and (b) phosphorus, in living and newly abscised leaves. The difference in nutrient concentration between living and abscised leaves indicates the extent of nutrient resorption prior to abscission. Values are means (and standard errors) of three blocks, each comprising composite samples from five trees (living leaves) or three litter traps (abscised leaves).

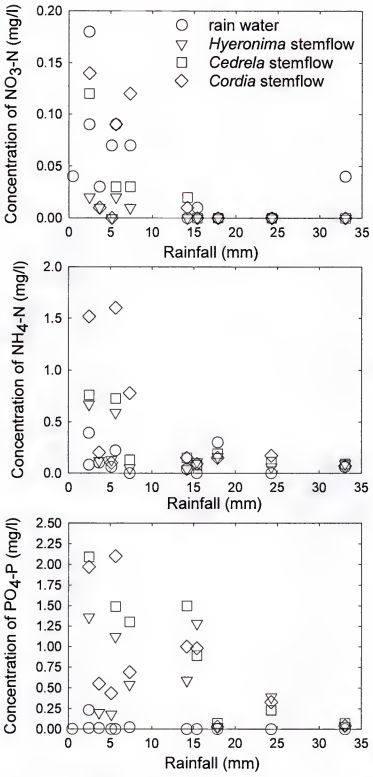

Figure 4-2 (a) Concentrations of NO_3-N, NH_4-N and PO_4-P in stemflow and rainwater relative to rain-event size. Each point represents a mean of 14 to 18 individuals sampled. (b) Concentrations of NO_3-N, NH_4-N and PO_4-P in throughfall and rainwater relative to rain-event size. Each point represents a mean of five funnels sampled. (Note scale differences between Figures 4-2 (a) and (b) for NH_4-N and PO_4-P.)

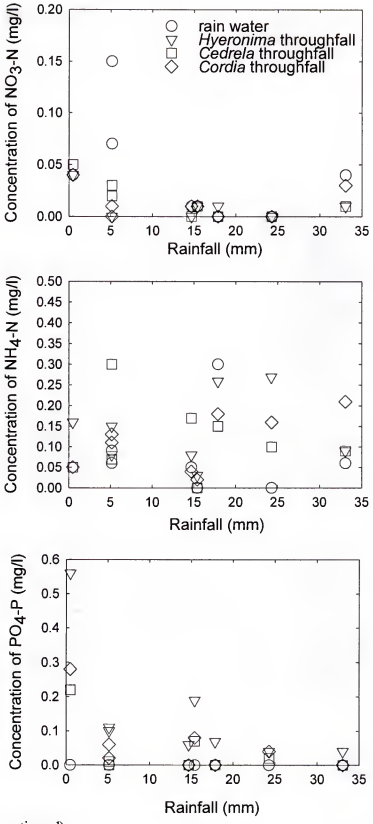

Figure 4-2 (continued).

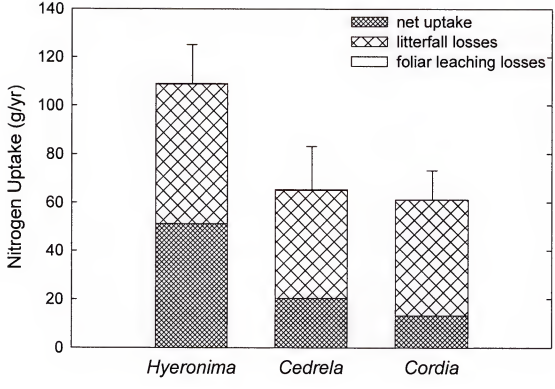

Figure 4-3. Total nitrogen uptake by average individuals of the three species. Values are means (standard errors) of three blocks. Foliar leaching losses are too small to show at this scale.

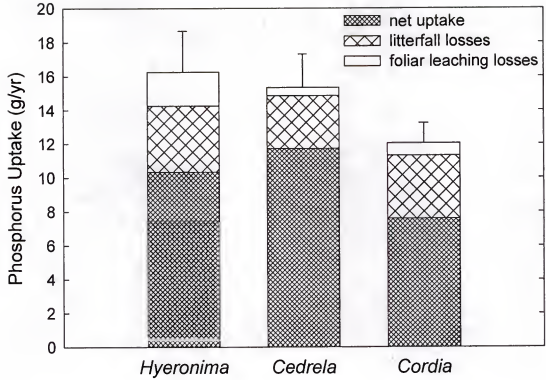

Figure 4-4. Total phosphorus uptake by average individuals of the three species. Values are means (standard errors) of three blocks.

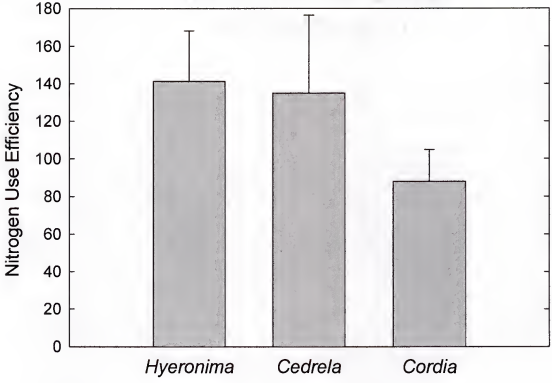

Figure 4-5. Nitrogen use efficiency of average individuals of the three species. Nitrogen use efficiency is the ratio of aboveground NPP to total nitrogen uptake. Values are means (standard errors) of three blocks.

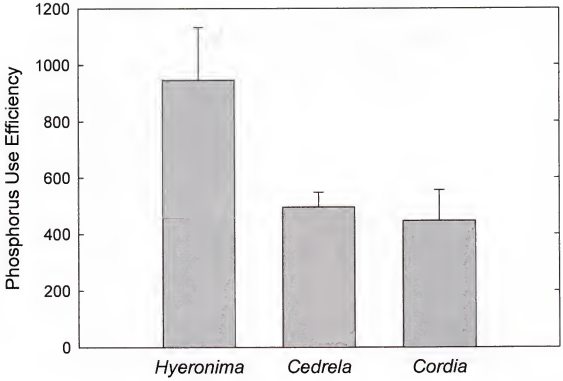

Figure 4-6. Phosphorus use efficiency of average individuals of the three species. Phosphorus use efficiency is the ratio of aboveground NPP to total phosphorus uptake. Values are means (standard errors) of three blocks.

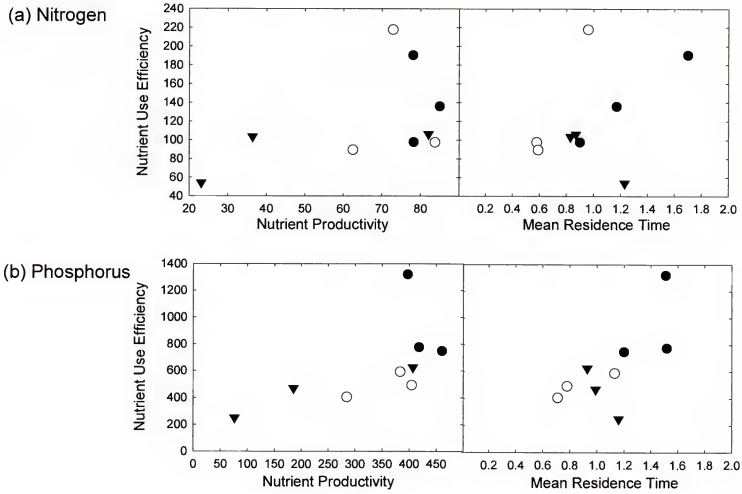

Figure 4-7. Nutrient use efficiency as a function of nutrient productivity (g/g) and mean residence time of nutrients (yr) for (a) nitrogen and (b) phosphorus.

CHAPTER 5
NUTRIENT USE EFFICIENCY AT THE ECOSYSTEM LEVEL

Introduction

Ecosystem nutrient use efficiency is a measure of ecological functioning that integrates ecosystem productivity and nutrient retention. The high productivity and nutrient retention observed in natural ecosystems is often attributed to high species diversity. In some experimental systems it is shown that the addition of species leads to added productivity (Willey 1985, Naeem et al.1994, Hooper 1998) and that greater diversity leads to greater nutrient retention (Ewel et al. 1991, Tilman et al. 1996, Hooper 1998, Hooper and Vitousek 1998). Nevertheless, contrary evidence indicates that some single-species systems can be as productive as diverse systems (Ewel 1999) and can develop root systems that are as effective at resource capture as more complex systems (Berish and Ewel 1988). What are the mechanisms that underlie high ecosystem productivity and nutrient retention, consequently high ecosystem nutrient use efficiency?

Ecosystem nutrient use efficiency is defined as the ratio of net primary productivity to the rate of soil nutrient supply:

$$Ecosystem\ NUE = \frac{NPP}{Soil\ Nutrient\ Supply} \quad (1)$$

This expression can be further expanded as follows (see Bridgham et al. 1995):

$$Ecosystem\ NUE = \frac{NPP}{Nutrient\ Uptake} \times \frac{Nutrient\ Uptake}{Soil\ Nutrient\ Supply} \quad (2)$$

Ecosystem nutrient use efficiency therefore depends on two component indices, a) plant-level nutrient use efficiency (i.e., net primary productivity of the individuals that make up the system per unit of nutrient taken up by them; Hirose 1975) and b) uptake efficiency (i.e., total uptake by the individuals that make up the system per unit of nutrient supplied by the soil; Shaver and Melillo 1984).

Plant-level nutrient use efficiency (i.e., net primary productivity per unit nutrient uptake) depends on productivity per unit of nutrient in the plant and mean residence time of nutrients (Berendse and Aerts 1987). Mean residence time of nutrients is a function of tissue turnover and nutrient resorption by the plant prior to tissue abscission. Nutrient use efficiency of the individuals composing the system can influence ecosystem nutrient use efficiency both in the short term and in the long term. In the short term, plant nutrient use efficiency has implications for competitive interactions among species, which in turn has feedbacks to nutrient use efficiency of the system as a whole. Tilman et al. (1997) suggest that plants with high nutrient use efficiency have a higher competitive ability and can tolerate lower nutrient availabilities, and so be more productive in diverse, competitive environments. A system made up of individuals with high competitive abilities can therefore have a higher productivity per unit of nutrient supplied by the soil than one made up of individuals with low nutrient use efficiencies and lower competitive abilities.

Over the longer term, plant nutrient use efficiency can influence ecosystem nutrient use efficiency through its influence on nutrient uptake rates and litter nutrient

return (Hobbie 1992). High nutrient use efficiency at the plant level goes hand in hand with a high degree of nutrient conservation in the plant. A low rate of litter nutrient return implies reduced nutrient availability at the ecosystem level due to the slower breakdown of low-quality litter (Aber and Melillo 1982, Melillo et al.1982, Schlesinger 1991), therefore greater immobilization and nutrient retention in soil in the long term (Tilman et al. 1997).

The other component of ecosystem nutrient use efficiency, uptake efficiency (i.e., the ratio of nutrient uptake to soil nutrient supply), can also influence nutrient retention. The larger the proportion of the soil's nutrient supply that is taken up by plants and sequestered in biomass, the smaller the proportion that remains to be potentially lost from the soil by leaching (Shaver and Melillo 1984). High total nutrient uptake can be achieved if species are separated in their resource requirement and are therefore able to partition the total resource supply. One way is temporal separation of species in their resource requirement (e.g., the early phenology of spring flowers in the understory of temperate deciduous forests [Muller 1974]). Another way is spatial separation of species in their resource requirement (e.g., the access to water from different soil depths by roots of evergreen and deciduous species [Jackson et al. 1995]). In addition, high total uptake can be achieved if species differ in their resource requirements, either by taking up resources in different proportions (e.g., as demonstrated theoretically by Tilman [1988]) or by relying on different forms of the same nutrient (e.g., the use of inorganic soil nitrogen and diatomic nitrogen fixed by associated bacteria in mixtures of non-legumes and legumes, respectively, as demonstrated by Martin and Snaydon [1982]).

It follows therefore, as suggested by Tilman et al. (1997) in the context of diversity and ecosystem productivity, and by Hooper (1998) in the context of diversity and nutrient retention, that ecosystem nutrient use efficiency depends on the identity of the species making up the system, and not on a greater diversity of species, per se. A combination of species with a high plant-level nutrient use efficiency, consequently higher competitive abilities, should lead to high relative productivity per unit of nutrient available. Furthermore, a combination of species that is able to partition the available resource supply should lead to high total uptake per unit of nutrient available.

I investigated ecosystem nutrient use efficiency for nitrogen (N) and phosphorus (P) in experimental ecosystems of varying lifeform composition. The systems were tree monocultures and diverse systems that contained a tree species planted with species of two additional lifeforms, both large, multistemmed, perennial monocots: a woody palm (*Euterpe oleraceae*) and a herb (*Heliconia imbricata*), in an additive design (Chapter 2). The experiments were replicated three times, each characterized by a different tree species—*Hyeronima alchorneoides*, *Cedrela odorata,* and *Cordia alliodora*. I made the following predictions for ecosystem nutrient use efficiency:

Prediction 1. Ecosystem nutrient use efficiency of the tree monocultures follows the pattern *Hyeronima* monocultures > *Cedrela* monocultures > *Cordia* monocultures.

Rationale. Because ecosystem nutrient use efficiency is partially a function of plant-level nutrient use efficiency (equation 2), efficiency at the ecosystem level should reflect efficiency at the plant level (Chapter 4).

Prediction 2. Ecosystem nutrient use efficiency of the diverse systems (hereafter also referred to as the polycultures) follows the pattern *Hyeronima*-dominated systems > *Cedrela*-dominated systems > *Cordia*-dominated systems.

Rationale. High nutrient use efficiency of the dominant tree species imparts greater competitive ability at the higher planting densities in the polycultures. Therefore productivity, consequently nutrient use efficiency, of polycultures should reflect the relative differences in nutrient use efficiency among their respective dominant tree species.

Prediction 3. Nutrient retention in biomass and in the soil follows the pattern diverse systems > monocultures.

Rationale. Total nutrient uptake per unit of nutrient available should be greater in the diverse systems due to partitioning of available resources by plants of the different lifeforms. Therefore, nutrient retention by the polycultures should be higher than by their respective monocultures, due to greater sequestration of nutrients in biomass. Furthermore, in the diverse systems, the additional monocots are likely to influence rates of nutrient supply. Palms, especially, produce litter that decomposes slowly (Ewel 1976). Over time, therefore, differences in litter quality between monocultures and polycultures should lead to greater nutrient immobilization in the soil, accompanied by lowered rates of nutrient supply in polycultures.

Ecosystem nutrient use efficiency was calculated as the ratio of aboveground net primary productivity to soil nutrient supply. Uptake efficiency was inferred from the ratio of total aboveground nutrient accrual to soil nutrient supply. Although differences in litter quality and its consequences for rates of decomposition and nutrient immobilization were

not investigated directly, indices of soil nutrient availability were examined for differences among species and treatments as hypothesized above.

Methods

Net Primary Productivity and Nutrient Accrual

Annual aboveground NPP for each year from mid-1993 to mid-1997 was estimated for all monocultures and polycultures. Mid-1993 was chosen as the starting point for this study, because the tree species had not closed canopies prior to the 1993-94 measurement interval (canopy closure occurred at 10, 14, and 16 mo for *Cordia*, *Hyeronima*, and *Cedrela*, respectively; Haggar and Ewel 1995); canopy closure is associated with a shift from a greater reliance on nutrient uptake from the soil to a greater reliance on internal nutrient recycling, thereby marking a change in plant nutrient use efficiency (Miller 1984). NPP was calculated as the algebraic sum of annual aboveground biomass increment and annual litterfall. Litter was collected biweekly from three 1.73 x 0.50 m traps in each plot, combined, separated by species, then dried at 70 °C and weighed.

Aboveground biomass of trees (stems, branches, petioles or rachises, and leaves), palms (stems and fronds), and *Heliconias* (petioles and leaf blades) was determined using allometric equations relating biomass to plant size. The general form of the allometric equations used was $\log W = \log a + b \log X$, where W is biomass of the fraction being assessed and X is a compound measure of plant size (Satoo and Madgwick 1982). Tree biomass was best predicted by either $X = HD^2$ or HD (H = height, and D = diameter); palm biomass was best predicted by $X = HD$ or HDF (where F is the number of fronds);

and *Heliconia* biomass was best predicted by $X = HR$ (where R is the number of ramets). The r^2-values obtained ranged from 0.47 to 0.94.

Starting in 1991, 24 individuals of each tree species and 18 individuals of each monocot species were harvested annually from zones specifically designated for destructive sampling in the study plots. (The number of harvested trees was reduced to 18 in 1993, and 6 in 1996; the number of harvested monocots was reduced to 9 in 1996.) Harvested plants were separated into their biomass components, fresh mass of each component was determined in the field, and a subsample of each component was dried to constant weight at 70 °C and weighed to obtain the wet-to-dry mass conversion factor for total fresh biomass. Equations were modified annually as larger individuals were added to the data set with each new biomass harvest. Inventories of plant size (height and diameter for trees; height, diameter, and number of fronds for palms; and height and number of ramets for *Heliconias*) in June-July of each year provided input to the allometric equations.

Annual aboveground accrual of N and P was calculated as the difference between nutrient standing stocks at the beginning and end of a measurement interval. Nutrient standing stocks were estimated as the product of nutrient concentration in each biomass fraction times the standing biomass of each fraction. Nutrient concentrations were determined on tissue subsamples of individuals harvested annually to provide data for the allometric equations. Tissue samples were dried at 70 °C, ground to pass a 2 mm sieve and analyzed for total N and P (Tabatabai and Bremmer 1991). Nutrient standing stocks for each year were calculated based on nutrient concentration of tissues harvested in that

year, with the exception of nutrient standing stocks for 1997, which were calculated based on nutrient concentration of tissues harvested in 1996.

Soil Nutrient Supply

Soil N supply was assessed every 4 mo by measuring net N mineralization and nitrification by *in situ* incubations of isolated soil cores (Anderson and Ingram 1989). Two pairs of cores, each 10 cm in diameter and 20 cm deep, were sampled in every plot. The two pre-incubation cores per plot were combined, and 15 g of soil from the resulting composite sample were extracted with 100 ml of 2M KCl by shaking for 1 hr. The extract was then filtered, and the filtrate was analyzed for NH_4-N and NO_3-N using automated colorimetry (Technicon 1973). The other two cores in every plot were incubated *in situ* for 21 d, after which they were removed and processed in a manner identical to the initial, pre-incubation cores. Rates of net N nitrification ($NO_3\text{-}N_{final} - NO_3\text{-}N_{initial}$) and mineralization ($[NO_3\text{-}N_{final} + NH_4\text{-}N_{final}] - [NO_3\text{-}N_{initial} + NH_4\text{-}N_{initial}]$) were calculated as described in Haggar and Ewel (1994). Data on extractable NH_4-N were not available for all sampling dates due to analytical difficulties. Therefore, net N mineralization could not be estimated for all sampling dates; instead, nitrification rate was used as the index of soil N supply in calculations of stand N use efficiency. Net nitrification corresponding to each NPP measurement was estimated by averaging the three assessments of nitrification made during the year.

Soil P supply was characterized using several different indices. One index used was extractable P obtained using an EDTA-modified bicarbonate extraction (modified Olsen extraction; Hunter 1974). Soil was sampled annually by coring to a depth of 70 cm. Three cores were sampled per plot, and cores were combined by depth (0-10, 10-25, and

25-70 cm). Soil was air dried and ground to pass a 2 mm sieve; 2.5 g of soil were extracted with 25 ml of the extraction solution by shaking for 10 minutes, and the extract was analyzed for P colorimetrically (Murphy and Riley 1962). Extractable P was subsequently summed over the entire soil volume sampled using soil bulk densities measured by Weitz et al. (1997). The resulting value of soil P (in g/m^2) was used as the index of soil P supply in calculating stand nutrient use efficiency with respect to P.

In 1996, two additional indices of extractable P—bicarbonate extractable P and dilute acid-fluoride extractable P—were determined on soils sampled to a depth of 25 cm (0-10 and 10-25 cm). The bicarbonate extractions were conducted on field moist soil that had been stored at 4 °C. Microbial P (P_m) was determined using a modification of the method of McLaughlin et al. (1986). Three 2.5 g subsamples of soil (one that was fumigated with 1 ml chloroform at 25 °C for 48 hr, a non-fumigated control, and a non-fumigated recovery control that was spiked with a known amount of P) were extracted by shaking for 1 hr with 25 ml 0.5 M $NaHCO_3$ and centrifuged, and the supernatant was analyzed for P colorimetrically (Murphy and Riley 1962). Inorganic P (P_i) was determined from the non-fumigated controls. P_m was determined as the difference between the fumigated sample and the non-fumigated control, taking into account the percent recovery of the added spike. In addition, a 5 ml aliquot of the supernatant from the non-fumigated control was evaporated at 105 °C and digested with concentrated HCl. The resulting digest was then analyzed for total P, and organic P (P_o) was determined as the difference between total P and P_i.

The second set of extractions, using dilute acid-fluoride (Bray and Kurtz extraction; Olsen and Sommers 1982), was conducted on air-dried soil that had been

ground to pass a 2 mm sieve. Soil (1 g) was extracted with 7 ml of the 0.03 N NH_4F-0.025 N HCl extracting solution for 1 min and centrifuged, and the supernatant was analyzed for inorganic P (Murphy and Riley 1962).

Statistical Analysis

Interspecific (i.e., among the dominant tree species, *Hyeronima*, *Cedrela* and *Cordia*) and between-treatment (monoculture or polyculture) differences in means of NPP, nutrient standing stocks, soil nutrient supply, and nutrient use efficiency were analyzed using analysis of variance. Analysis of variance was performed with PROC Mixed in SAS (SAS Institute 1997). Species, treatment, and their interactions were treated as fixed effects; time was treated as a fixed, repeated measure; and block and its interactions with species and time were treated as random effects. Compound symmetry (CS) covariance structure was used, which assumes that variance is constant over time. Model residuals were examined to ensure that the assumption of equal variances was not violated. In cases where variance increased as a function of the mean, the data were log-transformed.

For the additional measurements of soil P conducted in 1996, a split-plot analysis of variance was used to examine interspecific and between-treatment differences in mean extractable P. Tree species were treated as whole-plot effects, with treatments as subplots. Split-plot analysis of variance was performed with the GLM procedure in SAS (SAS Institute 1988).

Results

Aboveground NPP

Over the 4 yr of the study, aboveground NPP ranged from about 1.9 to 8.8 g m^{-2} d^{-1} (equivalent to 7 to 32 Mg ha^{-1} yr^{-1}; Figure 5-1). NPP was consistently high (>18 Mg ha^{-1} yr^{-1}) in the *Hyeronima*-dominated systems—both monocultures and polycultures—over the entire duration of the study. In the first 3 yr there was no discernible difference in productivity between the two *Hyeronima* treatments due to the nearly identical productivity of the trees in both treatments and the negligible contributions of *Euterpe* and *Heliconia* to total productivity in the diverse systems. In the fourth year the treatments began to diverge as productivity in the polycultures surpassed the monocultures, although the difference between the treatments during this interval (1996-1997) was not significant. The increase in productivity in *Hyeronima* polycultures relative to *Hyeronima* monocultures in the fourth year was due to an almost ten-fold increase in *Euterpe* productivity from 1995 to1997 and a five-fold increase in *Heliconia* productivity from 1996 to 1997.

In the *Cedrela*- and *Cordia*-dominated systems productivity varied practically two-fold over the duration of the study. Productivity of the diverse *Cedrela*- and *Cordia*-dominated systems was extremely high in the first and fourth years (> 23 Mg ha^{-1} yr^{-1}), and was significantly higher than that of the monocultures. For the two intervening years, on the other hand, neither the *Cedrela*- nor the *Cordia*-dominated systems showed any between-treatment difference in productivity. The striking difference in productivity between monocultures and the diverse systems in the first year was due almost entirely to the *Heliconias*, while the difference in productivity between monocultures and

polycultures in the fourth year was due largely to the palms. Furthermore, unlike in the *Hyeronima*-dominated systems, both in the *Cedrela*- and in the *Cordia*-dominated systems, tree productivity showed marked differences between monocultures and diverse systems. For *Cedrela,* tree productivity was the same at the outset, but gradually diverged as productivity of trees in the diverse systems dropped below that of trees in monoculture. For *Cordia,* on the other hand, productivity of trees in monoculture was higher than in the diverse systems at the start of the study, but gradually converged with a decline in productivity of trees in monoculture.

Soil Nutrient Supply

Net N mineralization and nitrification measured over the 4 yr of the study averaged about 0.26 and 0.23 $\mu g\ g^{-1}\ d^{-1}$, respectively (Figures 5-2, 5-3). This is equivalent to N mineralization and nitrification of the order of 120-135 $kg\ ha^{-1}\ yr^{-1}$. There was significant temporal variation both in rates of N mineralization and nitrification, but there were no differences among species or treatments although there was a weak interaction between them.

Nitrification rates were used to estimate an annual rate of soil N supply. Nitrification rates rather than net N mineralization rates were used because NH_4-N analyses necessary for calculating mineralization rates were not available for the entire study period, and because nitrification accounted for most of N mineralization in these systems (cf Figures 5-2, 5-3). Annual N supply (estimated by averaging the three measurements of nitrification made during the year) decreased with time for all species and treatments. Annual rates of soil N supply in *Hyeronima*-dominated monocultures were consistently lower than in the diverse treatments, but these differences were not

significant. In the *Cedrela*- and *Cordia*-dominated systems, on the other hand, the relative difference between the treatments was not consistent over the duration of the study, although the monocultures showed a trend toward higher soil N supply than the polycultures.

Values of modified Olsen-extractable P ranged from about 2.5 to 8.0 g/m^2 (Figure 5-4). There was a significant effect of treatment, although the effect of treatment on Olsen-extractable P was consistent neither across species nor from one year to the next between treatments dominated by the same tree species. Nevertheless, there was a significant increase in Olsen-extractable P over time (in 1996 compared with previous years) and this pattern was observed for all species and treatments.

A more detailed additional analysis of soil P was conducted in 1996 using several indices (bicarbonate-extractable P_i, P_m, P_o, and acid-fluoride extractable P). Values of P in mg/kg were of the order 4 to 7 (P_o), 7 to 15 (P_i), 10 to 15 (acid-fluoride extractable P), and 7 to 20 (P_m). None of these indices showed any significant effect either of dominant tree species or of treatment (Figure 5-5).

Nutrient Accrual and Uptake Efficiency

Aboveground standing stocks of N and P grew from initial values of 10 and 2 g/m^2, respectively, at the start of the 1993-94 measurement interval, to approximately 60 and 16 g/m^2, respectively, by the end of the 1996-97 measurement interval (Figures 5-6, 5-7). The dominant tree species exerted a significant effect with respect to N: standing stocks of N in the *Hyeronima*-dominated monocultures were higher than in the *Cedrela*- and *Cordia*-dominated monocultures at the start of the 1993-94 measurement interval and

at the start of the 1995-96 measurement interval. On the other hand, there was no species effect on P accrual among the three monocultures.

The presence of the monocots had a marked effect on aboveground accrual both of N and of P in the *Cedrela*- and *Cordia*-dominated polycultures, but not in the *Hyeronima*-dominated polycultures. At the start of the 1993-94 measurement interval there were no differences in aboveground N and P between the *Cedrela*- and *Cordia*-dominated monocultures and polycultures, but by the end of this interval they were strikingly different. The large pulse of productivity on the part of the monocots during this period lead to an almost three-fold increase in aboveground N and P. Furthermore, standing stocks of N and P remained high in the *Cedrela*- and *Cordia*-dominated polycultures even though total productivity dropped during the next two measurement intervals (1994-95 and 1995-96, Figure 5-1). During this time, there was a decline in standing stocks of *Heliconia* N and P due to a die-back of *Heliconia*, but this was more than compensated by an increase in standing stocks of *Euterpe* N and P.

Nutrient uptake efficiency, estimated as the ratio of aboveground nutrient accrual to soil nutrient supply, varied widely among species, treatments, and years (Figures 5-8, 5-9). Overall, there was a significant effect of dominant tree species on uptake efficiency for N and P. Treatment had a significant effect on N uptake efficiency, with marked increases in N uptake efficiency by the *Cedrela*- and *Cordia*-dominated polycultures during 1993-94 and 1996-97, but the effect of treatment on P uptake efficiency was not significant. Furthermore, nutrient uptake efficiency, as defined here, could not be calculated for all systems in all years, because there was no net accrual of N and P in aboveground biomass in some years (e.g., *Hyeronima*-dominated systems in 1993-94,

Cedrela-dominated polycultures in 1994-95, 1995-96, and *Cordia*-dominated polycultures in 1996-97).

Nutrient Use Efficiency

Ecosystem N use efficiency varied as much as ten-fold across species, treatments, and years (Figure 5-10). There was a steady increase in N use efficiency in the *Hyeronima*-dominated systems over time, but not in the systems dominated by the other two species. In monocultures, the dominant tree species exerted a significant effect—*Hyeronima* ecosystem N use efficiency was higher than that of *Cedrela* and *Cordia*, which did not differ from one another. The effect of the additional lifeforms, on the other hand, was significant in the *Cedrela*- and *Cordia*-dominated systems, but not in the systems dominated by *Hyeronima* (Table 5-1).

Ecosystem P use efficiency ranged from about 0.5 to 2.5 (Figure 5-11). P use efficiency showed a decreasing trend with time and was significantly lower by the fourth year of the experiment—the opposite of the pattern observed for N use efficiency. Ecosystem P use efficiency of the *Hyeronima*-dominated treatments was significantly greater than that of *Cedrela*-dominated treatments, which in turn was greater than the *Cordia*-dominated treatments. The additional lifeforms had no effect on P use efficiency of the *Hyeronima*-dominated systems, but they did affect P use efficiency by the *Cedrela*- and *Cordia*-dominated systems.

Discussion

Nutrient Use Efficiency

Nutrient use efficiency with respect both to N and P varied inversely with nutrient availability across all simple and diverse systems taken together (which is to be expected, because calculation of nutrient use efficiency includes nutrient availability; Figures 5-12, 5-13). This is similar to the pattern observed for a range of tropical and temperate forest ecosystems (Vitousek 1982, 1984), although the indices used to estimate nutrient use efficiency and nutrient availability differed. Vitousek (1982, 1984) estimated nutrient use efficiency as the ratio of litterfall mass to litterfall nutrient content and inferred nutrient availability from amounts of N and P returned to soil in litterfall.

Ecosystem N use efficiency measured in this study (100-1000) spans the ranges reported in other studies. Lennon et al. (1985) and Bridgham et al. (1995) estimated N use efficiency as the ratio of aboveground NPP to mineralization rate. Their values ranged from about 70-240. The difference between N use efficiency of the study systems and other reported values was primarily due to the much higher aboveground NPP of these tropical systems. Although rates of N supply in the study systems (~120 kg ha^{-1} yr^{-1}) were higher than those reported (~20-90 kg ha^{-1} yr^{-1}; Lennon et al. 1985, Bridgham et al. 1995), these rates are not unusually high when compared to values from elsewhere in the tropics. For example, Vitousek and Denslow's (1986) measurements of N mineralization in the neighboring forest at La Selva were of the order of 800 kg ha^{-1} yr^{-1}, and Smith et al. (1998) measured N mineralization rates of 195-328 kg ha^{-1} yr^{-1} in soils under tree plantations and adjoining forest in Brazil. Analogous estimates of ecosystem P use efficiency were not available for comparison with my estimates of P use efficiency.

Mechanisms

From plant to ecosystem. For monocultures alone, I predicted that ecosystem nutrient use efficiency would follow the pattern of plant-level nutrient use efficiency of the individual tree species, since ecosystem nutrient use efficiency is a function of nutrient use efficiency of the component species (equation 2). This prediction was only partly supported: With respect to N, plant level nutrient use efficiency followed a pattern of *Hyeronima* > *Cedrela* > *Cordia* (although it was not possible to detect significant differences among them; Chapter 4); ecosystem nutrient use efficiency of *Hyeronima* was high, as predicted, but there was no difference in nutrient use efficiency of *Cedrela*- and *Cordia*-dominated systems. With respect to P, plant level nutrient use efficiency followed a pattern of *Hyeronima* > *Cedrela* > *Cordia* (although *Cedrela* and *Cordia* P use efficiency were not significantly different; Chapter 4); ecosystem level nutrient use efficiency followed the same pattern.

Examining the relationship between ecosystem nutrient use efficiency and nutrient availability on a species-by-species basis showed distinct interspecific differences in the pattern of nutrient use efficiency as a function of nutrient availability described earlier (Figures 5-12, 5-13). N use efficiency of the *Hyeronima*-dominated systems increased with declining nutrient availability, but N use efficiency of the *Cedrela*- and *Cordia*-dominated systems appeared not to increase beyond a point (Figure 5-14). This pattern of increasing nutrient use efficiency down to some optimal nutrient availability, followed by a decline in nutrient use efficiency at sub-optimal nutrient availability is predicted by a theoretical model (Bridgham et al. 1995) and supported by data from a range of ecosystems (Lennon et al.1985, Bridgham et al. 1995). Lennon et al.

(1985) observed that the decline in productivity with declining N availability was accompanied by preferential investment of the limited N in leaf tissue with little N left over for production of new stem and root tissue. It is possible that, with the decline in N availability over the 4 yr of the study, both *Cedrela* and *Cordia* had reached the threshold beyond which ecosystem N use efficiency does not increase. Furthermore, higher plant-level nutrient use efficiency signals a tolerance of lower nutrient availability, therefore the level of N availability at which this threshold is reached should be highest for *Cordia* (with the lowest plant-level N use efficiency), intermediate for *Cedrela* (with intermediate plant-level N use efficiency), and lowest for *Hyeronima* (with the highest plant-level N use efficiency). This appears to be corroborated by the data (Figure 5-14). The continued increase in nutrient use efficiency of *Hyeronima*-dominated systems with a decline in N availability over the 4 yr of the study therefore explains why N use efficiency by these systems is higher than by *Cedrela*- and *Cordia* dominated systems.

A similar species-by-species analysis of ecosystem P use efficiency as a function of P availability suggests that low P availability at the start of this study may have marked the threshold for *Cordia*-dominated systems (Figure 5-15). This would account for the lower nutrient use efficiency in *Cordia*-dominated systems compared to *Cedrela*-dominated systems over the 4 yr of the study, despite the lack of difference in P use efficiency between them at the plant level.

In the case of the more diverse systems, productivity and nutrient use efficiency showed no consistent trends among species or treatments. I had predicted that productivity of the dominant tree species at the greater polyculture planting densities would be less affected in the case of trees with higher plant-level nutrient use efficiency,

since higher plant-level nutrient use efficiency signals a greater tolerance of reduced nutrient availability (Tilman et al. 1997). Therefore, nutrient use efficiency of *Hyeronima*-dominated polycultures would be higher than that of *Cedrela*-dominated polycultures, which in turn would be higher than that of *Cordia*-dominated polycultures. Although no consistent patterns were observed for either total productivity or N and P use efficiency of polycultures over the 4 yr, the results did support the hypothesis regarding differential effects of greater planting density on productivity of the dominant tree species (*Hyeronima* < *Cedrela* < *Cordia*) as predicted on the basis of their plant-level nutrient use efficiencies (*Hyeronima* > *Cedrela* > *Cordia*). Productivity of *Cordia* trees in polyculture dropped below that of trees in monoculture early in the course of the study (1993–94; Haggar and Ewel 1997), suggesting the early onset of competition from the co-planted monocots, and was significantly lower in 1994-95. The same pattern was observed for the *Cedrela*-dominated systems in the following year (1994-95), and by 1995-96 productivity of *Cedrela* trees in polyculture was significantly lower than that of trees in monoculture.

Koerselman and Meuleman (1996) suggested that the ratio of tissue N to P is an indicator of relative limitation by N and P. They demonstrated, in a survey of herbaceous species, that plant N:P < 14 signals relative N limitation, whereas N:P > 16 signals relative P limitation. N availability declined steadily over the duration of the study, presumably as a result of uptake and sequestration in biomass. P availability, on the other hand, increased over time. Therefore, these systems should become relatively more N than P limited over time. It follows that belowground competition, as inferred from changes in productivity of trees in monoculture compared to polyculture, should manifest

itself as a lowering of N:P. Whole-leaf nutrient concentrations of the study species did indeed indicate relatively greater limitation by N than by P (N:P = 9.8 in 1996) compared to N:P from a range of other tropical forest ecosystems, which suggest relatively greater limitation by P than by N (N:P = 17.3, Medina 1984; N:P = 21.4, Vitousek and Sanford 1986). A finer-scale sampling of foliar N and P using only leaf lamina disks (Chapter 3) supported the hypothesis of increasing N limitation over time. Furthermore, a comparison of N:P in foliage of trees in monoculture and polyculture (Table 5-2) showed that by 1995 both *Cordia* and *Cedrela*—but not *Hyeronima*—trees in polyculture had N:P < 14, suggesting N had becoming limiting to tree productivity in these systems.

Feedbacks to soil nutrient availability. I predicted that rates of soil nutrient supply would be influenced by nutrient use efficiency at the plant level. One way that high plant-level nutrient use efficiency is achieved is by a greater reliance on internal nutrient recycling—by greater tissue longevity and nutrient resorption prior to abscission—leading to a reduction in litter nutrient return to the soil (Berendse 1994). The resulting low-nutrient litter decomposes relatively slowly (Schlesinger 1991) due to greater nutrient immobilization by microbial biomass, leading to lowered rates of soil nutrient supply with less potential for nutrient losses from the system (Tilman et al. 1997).

For the dominant trees in the study systems, plant-level nutrient use efficiency varied about two-fold, while rates of tissue turnover—as inferred from measured leaf lifespan—varied as much as three-fold (Chapters 3, 4). Given the hypothesized links between plant-level nutrient use efficiency, tissue turnover, and soil nutrient supply, rates of soil nutrient supply in the monocultures should reflect differences in plant-level

nutrient use efficiency of the dominant tree species. Furthermore, in the diverse systems, the presence of the additional lifeforms—particularly palms with litter that is slow to decompose—should have added consequences for soil nutrient supply. Over time, therefore, there should be greater soil nutrient immobilization in polycultures, and rates of nutrient supply in polycultures should decline relative to the monocultures.

Although I did not directly investigate rates of litter decomposition, I was able to test these predictions regarding emerging differences in soil nutrient supply by examining indices of soil N and P. The predictions regarding differences in soil nutrient supply among monocultures and between monocultures and polycultures were not supported by the data either for N or for P. In the case of soil N, both net mineralization and nitrification showed a decreasing trend with time. This, presumably, was a result of changes in litter quality over time: it is demonstrated that as forest ecosystems develop there is a shift from greater nutrient cycling between plant and soil to a greater reliance on internal nutrient recycling within plants (Miller 1984). Initial extractable NO_3-N and NH_4-N also declined in all systems over time, presumably as a result of uptake and sequestration in biomass. Similar decreases in soil nutrients have been observed in other successional systems during the initial years of recovery after disturbance (Ewel et al. 1991). Nevertheless, there were no consistent trends in rates of soil nutrient supply when comparing monocultures dominated by the three tree species, or when comparing monocultures and polycultures dominated by the same tree species. Olsen-extractable P showed an increasing trend over time, which was the reverse of the pattern observed for soil N. This may have resulted from plant roots modifying the soil environment. For example, the exudation of organic acids by roots can lead to an increase in P availability.

Similarly, mycorrhizae associated with roots can alter soil P availability (Schlesinger 1991). It might be expected that the greatest increase in soil P would be observed at the soil surface: nutrients taken up from a large volume of soil by extensive root systems are returned to the soil in litter and can become aggregated in the surface layers. The increase in soil P observed in these systems, on the other hand, appeared to be weighted by increases in the deeper soil layers. Nevertheless, as with soil N, there were no consistent patterns in Olsen-extractable P when comparing monocultures or monocultures and polycultures. Furthermore, an investigation of soil P using several additional indices also failed to demonstrate any effect of dominant species or of the presence of the other lifeforms.

There is a great deal of evidence for the effect of plant species on soil nutrient supply from a suite of temperate and tropical ecosystems. For example, rates of N mineralization and nitrification were related to leaf lifespan and litter quality in a series of temperate tree plantations (Gower and Son 1992), to fine root nutrient content in tropical tree plantations (Smith et al. 1998), and to the quantity and quality of litter nutrient return in experimental temperate grassland ecosystems (Wedin and Tilman 1990). It is surprising, therefore, that differences in soil nutrient supply were not observed among the study systems. One possibility is that, despite the large variation in tissue turnover and nutrient use efficiency among the species in this study, these differences are small compared to the range of leaf lifespans (e.g., Reich et al.1991) and plant-level nutrient use efficiencies (e.g., studies reviewed in Chapter 4) encountered in nature. Therefore, the absolute differences among them may not be large enough to be manifested as differences in litter quality or rates of litter decomposition. Alternatively, it is possible that the

relatively high background levels of soil N and P at the study site (Chapter 2) compensate for low nutrient contents in litter, thereby masking the effects of differences in litter quality on litter decomposition. Although rates of litter decomposition are primarily controlled by litter quality, there is limited evidence that soil fertility can also exert an influence on rates of decomposition (e.g., as demonstrated by experiments with roots decomposed in sites subject to different fertilization treatments; Ostertag 1998).

Nutrient accrual and uptake efficiency. The uptake and sequestration of nutrients in biomass is an important means of preventing nutrient losses from an ecosystem via leaching from the soil (Nye and Greenland 1960, Vitousek and Reiners 1975). Nutrient uptake efficiency (i.e., uptake per unit nutrient available) is hypothesized to increase with decreasing nutrient availability, as demonstrated in experiments with a suite of marsh species (Shaver and Melillo 1984), although pine seedlings grown at different levels of N application showed greater N uptake with increasing N supply (Birk and Vitousek 1986). The study systems showed no consistent patterns between nutrient uptake and soil nutrient supply. I estimated uptake efficiency as the ratio of total aboveground nutrient accrual (i.e., net uptake) to soil nutrient supply, unlike other studies that estimate uptake efficiency as the ratio of total uptake (i.e., gross uptake) to soil nutrient supply. It is possible that a high proportion of nutrients supplied by the soil are being taken up and cycled between plant and soil, even though there is little or no net nutrient accrual in aboveground biomass (e.g., as in the *Hyeronima*-dominated systems).

Total aboveground nutrient accrual, rather than uptake efficiency, is a more relevant measure to assess nutrient retention by the study systems. I had predicted that the more diverse systems would have greater nutrient accrual in biomass, due to the

likelihood of partitioning of total nutrient supply by species of different lifeforms (or functional groups, e.g., Hooper 1998). Although the presence of the additional lifeforms had no effect on total nutrient accrual in the *Hyeronima*-dominated systems, in the *Cedrela*- and *Cordia*-dominated systems the monocots were responsible for a marked increase in total nutrient accrual in aboveground biomass. In *Cedrela*-dominated systems, particularly, the contribution of the monocots to total nutrient standing stocks was additional to that of the trees alone, whereas in *Cordia*-dominated systems nutrient accrual by the added monocots was accompanied by a decline in nutrient standing stocks of the trees in polyculture (Figure 5-7). This pattern parallels the complementary and compensatory patterns in productivity of trees and the additional lifeforms demonstrated for the *Cedrela*- and *Cordia*-dominated systems, respectively (Haggar and Ewel 1997) and supports the hypothesis that in the *Cedrela*-dominated systems, at least, the trees and the monocots may be partitioning the total nutrient supply.

Furthermore, in the *Cedrela*- and *Cordia*-dominated polycultures, total aboveground standing stocks of nutrients remained high despite a decline in standing biomass of the *Heliconia* (which has monocarpic ramets), with compensatory uptake of nutrients by the initially slower-growing palms during this period (1994-95 and 1995-96, Figures 5-6, 5-7). Such temporal partitioning in nutrient uptake is a potentially important mechanisms for nutrient retention as species replace one another in a successional sequence. The role played by *Heliconias*—with their rapid initial growth and early decline—in these perennial systems may be analogous to the vernal-dam role played by spring ephemerals in temperate deciduous woodlands in checking nutrient losses from the system prior to leafing out of the deciduous overstory on an annual cycle (Muller 1974).

Ecological Implications

Understanding the mechanisms that underlie ecosystem nutrient use efficiency is valuable not only for understanding the contribution of species diversity to ecosystem productivity and nutrient retention—both important measures of ecosystem functioning—but also for the design of human-managed ecosystems. Productivity per unit of nutrient supplied and ecosystem nutrient conservation are important management considerations, particularly in situations where reliance on external fossil-fuel subsidies for the maintenance of soil fertility may not be an economically viable option.

The role of species diversity in the functioning of ecosystems has received renewed interest in recent years, driven by the accelerating pace at which humans are altering and simplifying the global landscape (Naeem et al. 1994, Tilman and Downing 1994, Schulze and Mooney 1994, Orians et al.1996). One view arising out of this discussion is that species identity, and not diversity per se, is the key to high productivity and nutrient retention seen in many natural ecosystems. For example, Hooper (1998) demonstrated that which functional groups—not how many functional groups—of species were present had a greater effect on productivity in Californian serpentine grasslands. Similarly, Tilman et al. (1997) showed theoretically that the reason for higher productivity associated with higher diversity was because of the increased probability of species with certain characteristics occurring in the species mixture, and not just because of the total number of species present. Furthermore, the mechanisms of ecosystems nutrient retention may be related to the type of species present: in comparing plantations of similar ages, Silver et al. (1996) found that pine plantations had larger stores of nutrients in soil, whereas plantations of broadleaf trees had greater nutrient stores in

aboveground biomass, which they attributed to functional differences between the two groups (gymnosperms and angiosperms).

The results from this study also indicate that species may be important to processes at the ecosystem level. Ecosystem-level nutrient use efficiency was related to plant-level nutrient use efficiency of the dominant tree species. Furthermore, productivity of the dominant tree species in the more diverse systems appeared to be affected by their nutrient use efficiency. The species with the highest nutrient use efficiency, *Hyeronima*, showed the least reduction in productivity at the higher polyculture densities, whereas *Cordia*, the species with the lowest nutrient use efficiency, showed the greatest reduction in productivity. A further outcome of this study was the response of ecosystem nutrient use efficiency to changing nutrient availability over time. In studies along existing nutrient gradients, it is demonstrated that ecosystem nutrient use efficiency increases with decreasing nutrient availability down to some optimal value, after which there is no further increase in nutrient use efficiency (Lennon et al. 1985, Bridgham et al. 1995), and the systems in this study appeared to show a similar pattern. In addition, the results from this study indicate that this threshold nutrient availability at which the response of ecosystem nutrient use efficiency changes may be a function of nutrient use efficiency of the component species: *Hyeronima*, with the highest plant-level nutrient use efficiency showed increasing ecosystem nutrient use efficiency down to lower levels of nutrient availability that the other two species. This finding could be an important consideration in the choice of species to reforest lands that are inherently infertile, or in choosing species to grow on lands that have been greatly impoverished by past management practices.

Table 5-1. Results (probability values) of repeated measures analyses of variance on ecosystem nutrient use efficiency. (Bold numerals indicate significant effects [$p < 0.05$].)

Source	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Ecosystem N Use Efficiency	Ecosystem P Use Efficiency
Tree Species	2	4	**0.0198**	**0.0051**
Diversity	1	36	**0.0007**	**0.0002**
Year	3	6	**0.0313**	**0.0008**
Tree Species * Diversity	2	36	**0.0001**	**0.0433**
Tree Species * Year	6	36	0.1227	**0.0001**
Diversity * Year	3	36	**0.0001**	**0.0001**
Tree Species * Diversity * Year	6	36	**0.0056**	**0.0001**

Table 5-2. Ratios of foliar nitrogen to phosphorus for trees in monocultures and more diverse systems. Values are means (standard errors) of three blocks. Each measurement was based on analysis of leaf lamina disks from three leaves sampled from each of five trees. Values of N:P > 16 indicating relative P limitation are denoted in italics, and values of N:P < 14 indicating relative N limitation are denoted in bold numerals (after Koerselman and Meuleman 1996).

Year	*Hyeronima*		*Cedrela*		*Cordia*	
	monoculture	polyculture	monoculture	polyculture	monoculture	polyculture
1994	15.2 (0.5)	*18.1* (1.1)	*23.2* (1.9)	*22.9* (2.3)	*20.4* (1.2)	*17.6* (1.2)
1995	16.2 (1.0)	15.4 (1.3)	14.3 (0.8)	**13.4** (1.2)	14.7 (0.8)	**11.4** (1.4)

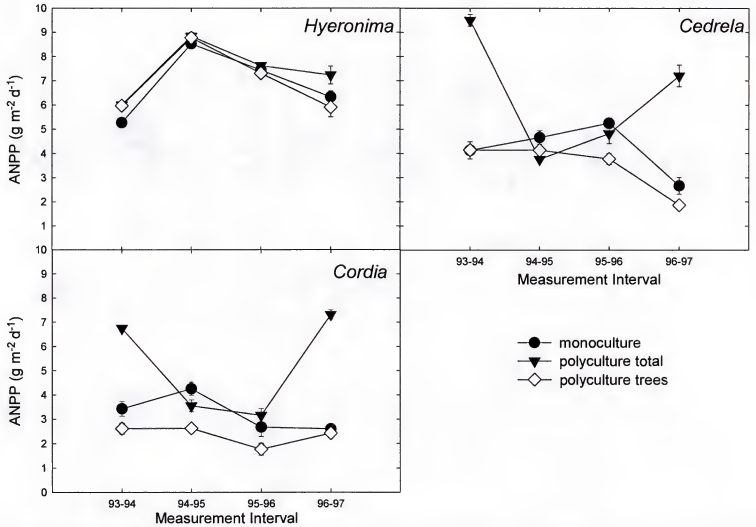

Figure 5-1. Aboveground net primary productivity in monocultures and polycultures. The difference between productivity by polyculture trees and total polyculture productivity is equivalent to productivity of the palms and *Heliconia*. Each point represents the mean (standard error) of three blocks.

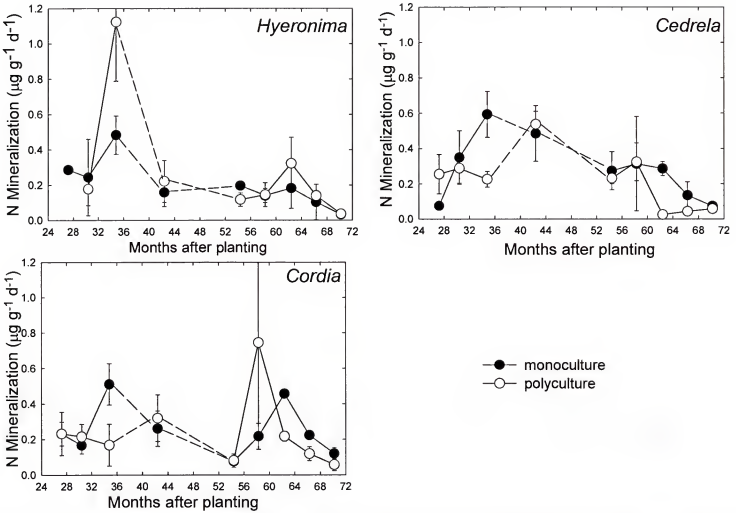

Figure 5-2. Rates of N mineralization measured every 4 mo in 21 d *in situ* incubations. Each point is a mean (standard error) of three blocks and combines soils sampled from two pre- and two post-incubation cores. (Dashed lines indicate missing mineralization estimates due to unavailability of ammonium anlayses).

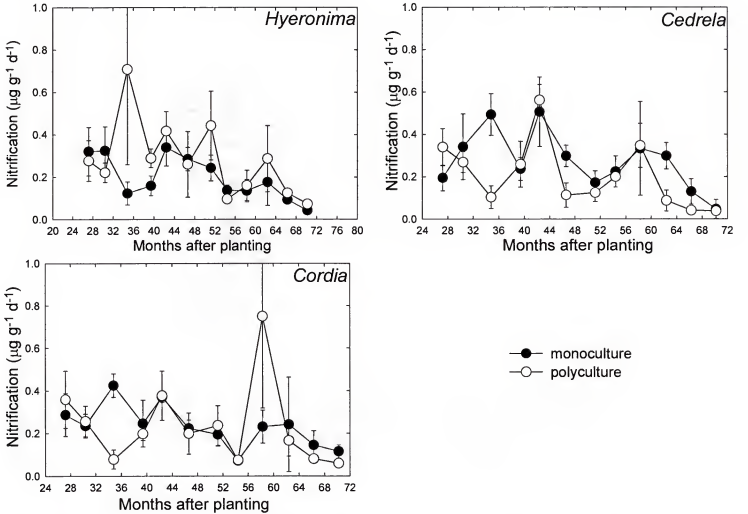

Figure 5-3. Rates of nitrification measured every 4 mo in 21 d *in situ* incubations. Each point is a mean (standard error) of three blocks and was based on composite samples of two pre- and two post-incubation soil cores.

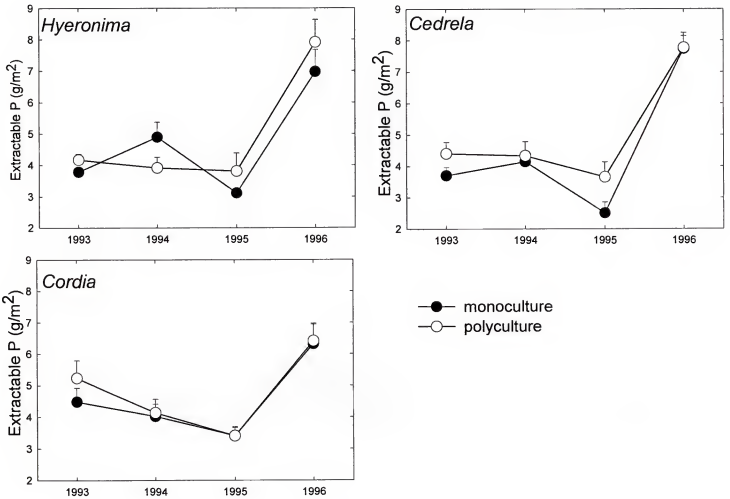

Figure 5-4. Olsen-extractable P measured annually. Points represent means (standard errors) of three blocks, each a composite sample of three cores. Cores were sampled to a depth of 70 cm (0-10, 10-25, and 25-70 cm). Results depicted here are values of soil P summed over the entire volume sampled.

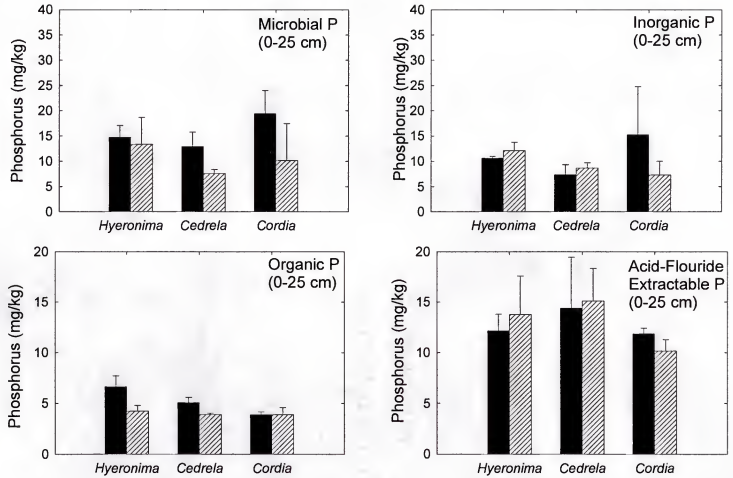

Figure 5-5. Indices of soil phosphorus sampled in 1996. All values are means (standard errors) of measurements from three blocks. Each measurement combines samples from three cores.

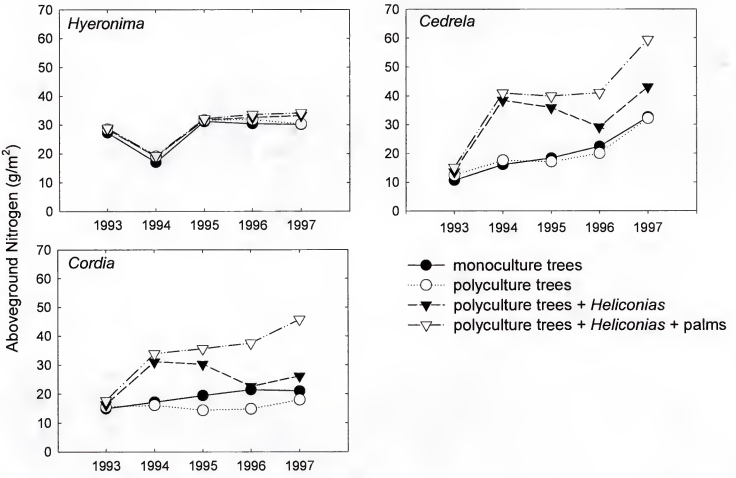

Figure 5-6. Changes in standing stocks of nitrogen in monocultures and polycultures dominated by the three tree species over the duration of the study. Each value respresents a mean of three blocks.

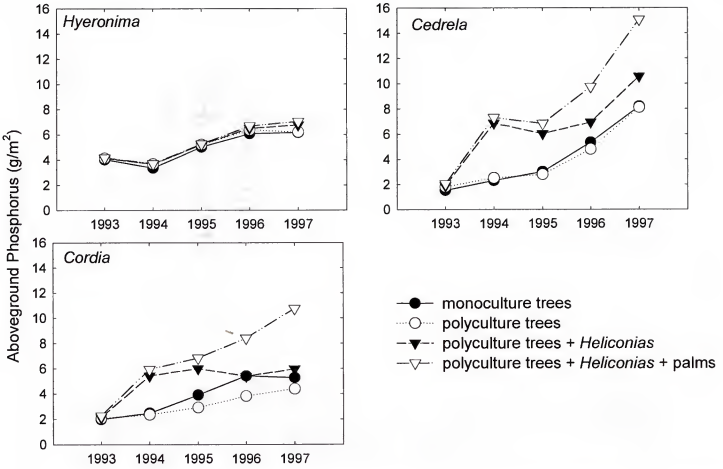

Figure 5-7. Changes in standing stocks of phosphorus in monocultures and polycultures dominated by the three tree species over the duration of the study. Each value respresents a mean of three blocks.

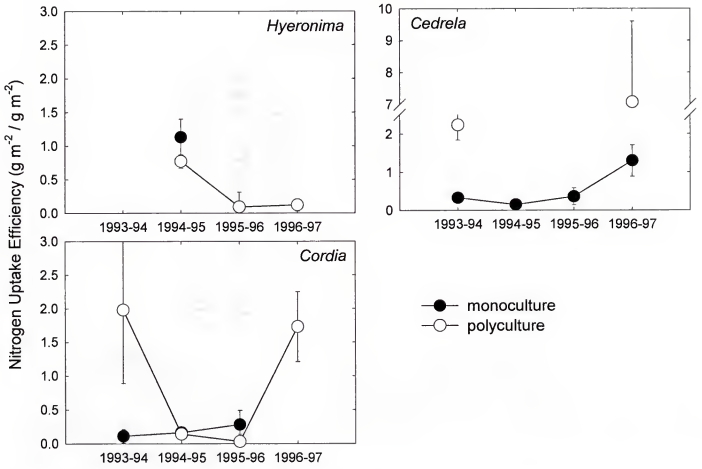

Figure 5-8. Nitrogen uptake efficiency calculated as the ratio of annual nitrogen accrued in aboveground biomass to an index of nitrogen supply (nitrification). Each value represents the mean of three blocks (with standard errors). Missing values are for intervals during which there was no net accrual of nitrogen in aboveground biomass.

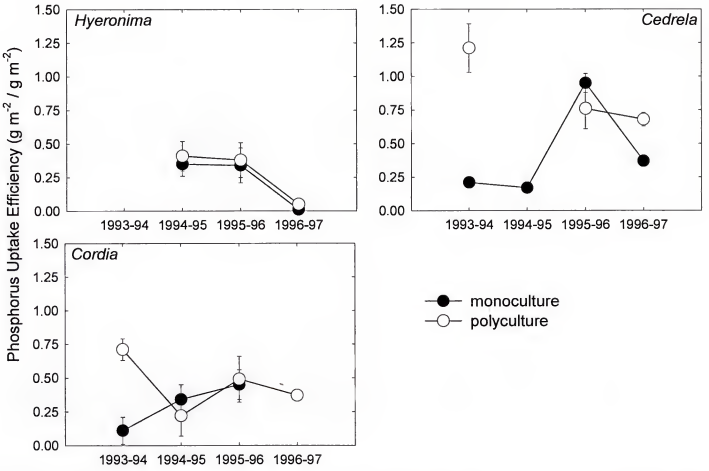

Figure 5-9. Phosphorus uptake efficiency calculated as the ratio of annual phosphorus accrued in aboveground biomass to an index of phosphorus supply (Olsen-extractable phosphorus). Each value represents the mean of three blocks (with standard errors). Missing values are for intervals during which there was no net accrual of phosphorus in aboveground biomass.

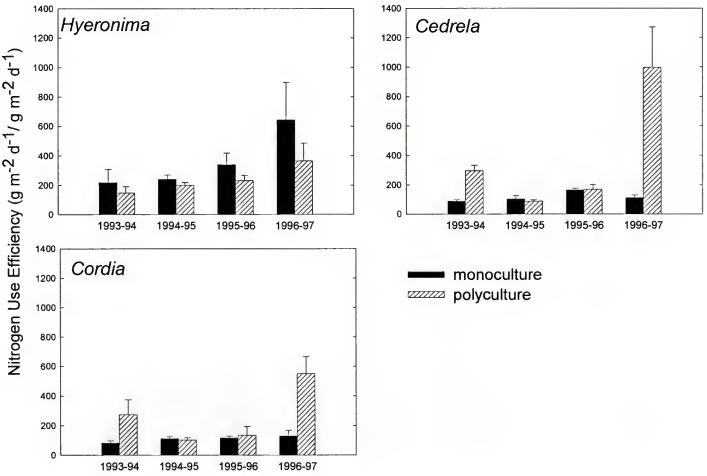

Figure 5-10. Ecosystem nitrogen use efficiency estimated as the ratio of net primary productivity to rate of nitrification. Values are means (standard errors) of three blocks.

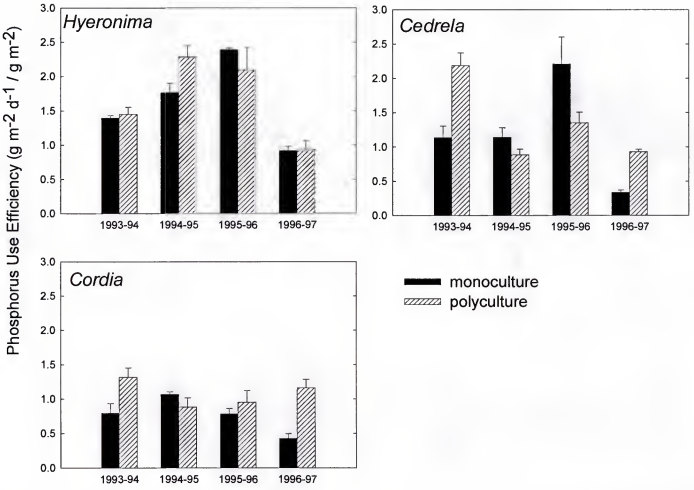

Figure 5-11. Ecosystem phosphorus use efficiency estimated as the ratio of net primary productivity to soil phosphorus (Olsen-extractable phosphorus was used as the index of soil phosphorus). Values are means (standard errors) of three blocks.

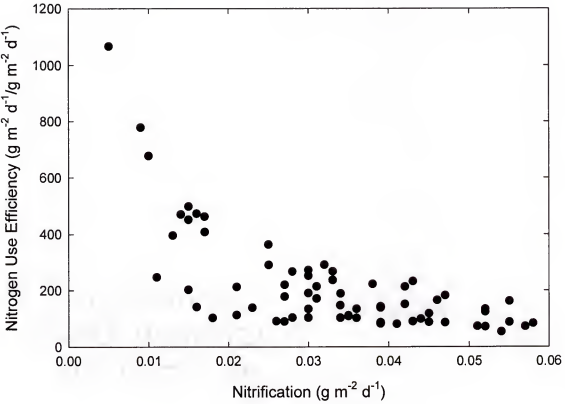

Figure 5-12. Ecosystem nitrogen use efficiency plotted against an index of soil nitrogen supply. Data from all species, treatments, and years are included.

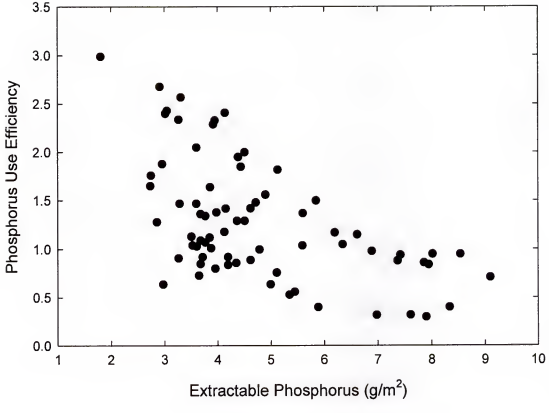

Figure 5-13. Ecosystem phosphorus use efficiency plotted against an index of soil phosphorus supply. Data from all species, treatments, and years are included.

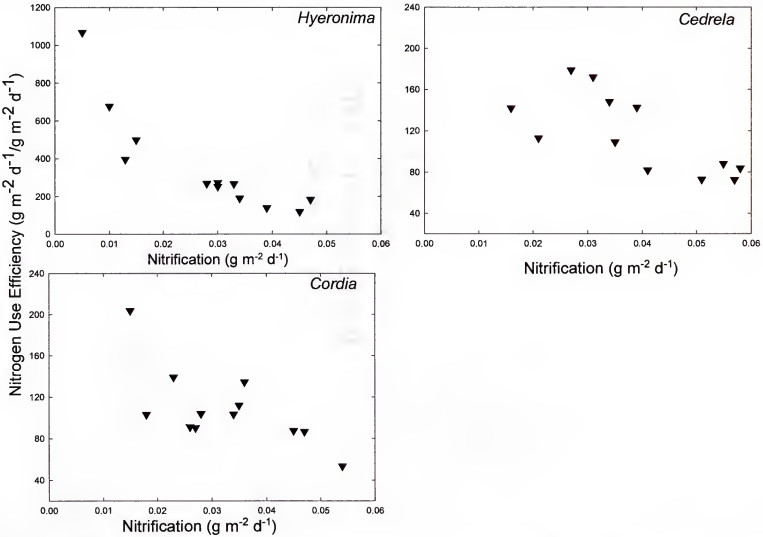

Figure 5-14. Ecosystem nitrogen use efficiency as a function of soil nitrogen supply (nitrification is used as the index of soil nitrogen supply). Only monoculture data are plotted.

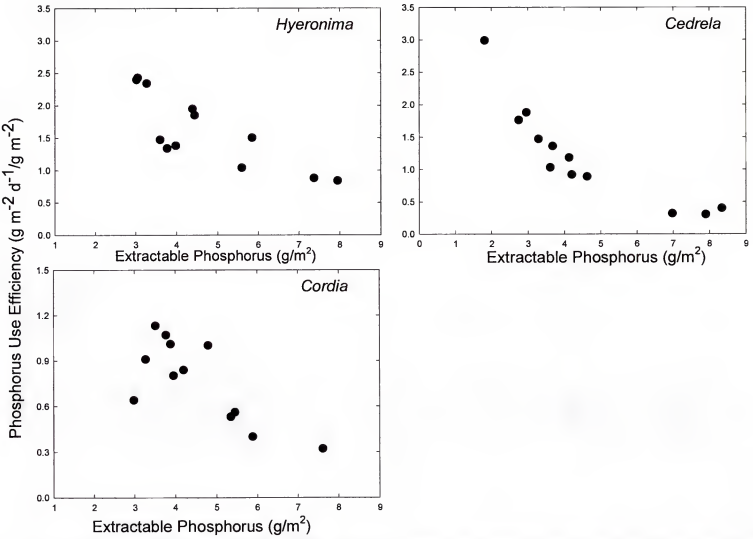

Figure 5-15. Ecosystem phosphorus use efficiency as a function of soil phosphorus supply (Olsen-extractable phosphorus is used as the index of soil phosphorus supply). Only monoculture data are plotted.

CHAPTER 6
CONCLUSIONS

Introduction

Nutrient use efficiency is a measure of physiological and ecological functioning that is applicable at scales from leaves to ecosystems. At every scale nutrient use efficiency integrates two components—productivity per unit of nutrient acquired and the effectiveness with which acquired nutrients are conserved. Ecologists have invoked differences in nutrient use efficiency among leaves and among plants to explain species' distributions within communities along small-scale environmental gradients (Small 1972, Rundel 1982, Chiba and Hirose 1993, Ellsworth and Reich 1996), and they have invoked differences in nutrient use efficiency among ecosystems to explain the distribution of communities along large-scale edaphic gradients (Vitousek 1982, 1984, Cuevas and Medina 1986, Silver 1994).

Although a high efficiency of nutrient use is likely to confer a competitive advantage to species in most situations, there may be exceptions in which high nutrient use efficiency has not been selected for. One such example is the case of ruderals in high nutrient, disturbed habitats, where high productivity and rapid reproductive output, rather than high nutrient use efficiency may be more beneficial (Chapin 1980). Another example is the case of species that take up and store nutrients in excess of amounts necessary for growth (luxury consumption; Chapin 1980). Despite their lower nutrient

use efficiency—calculated as biomass produced per unit nutrient uptake—such species may be at an advantage under conditions of reduced nutrient supply, by being able to draw on their reserves of stored nutrients. Nevertheless, where high nutrient use efficiency has been selected for, it is suggested that there are trade-offs between the two components of nutrient use efficiency—high productivity per unit of nutrient acquired and effective conservation of acquired nutrients—both of which vary widely in nature. Berendse and Aerts proposed (1987) that high-resource environments select for greater productivity per unit of nutrient acquired, and low-resource environments favor greater nutrient conservation. These two components of nutrient use efficiency are also desirable attributes in managed ecosystems, particularly in situations where external fertilizer subsidies are not always an option. Therefore, understanding the mechanisms that underlie nutrient use efficiency could help in achieving the proper mix of species that would lead to a high efficiency of nutrient use at all scales.

Cross-Scale Linkages in Nutrient Use Efficiency Revisited

Although a great deal is now known about nutrient use efficiency of leaves (Field and Mooney 1986, Evans 1989), plants (Hirose 1975, Berendse and Aerts 1987), and ecosystems (Lennon et al. 1985, Bridgham et al. 1995), little is known about relationships among measures of nutrient use efficiency at these different levels. There are strong parallels in the components of nutrient use efficiency at all levels. For example, photosynthesis (a leaf-level process) is the ultimate source of carbon for biomass production at the plant level, and biomass production (a plant-level process) contributes to total productivity at the ecosystem level. Similarly, leaf longevity and nutrient

resorption are linked to internal recycling of nutrients at the plant level, and internal recycling of nutrients by plants is linked to nutrient conservation at the ecosystem level. In fact, nutrient use efficiency of leaves is completely nested within nutrient use efficiency at the plant level, and nutrient use efficiency at the plant level is completely nested within nutrient use efficiency at the ecosystem level (Figure 6-1).

To what extent is it possible to predict nutrient use efficiency at one level from processes at the level below it? Alternatively, to what extent is nutrient use efficiency at each level controlled by larger scale processes that cannot be predicted from a knowledge of processes at smaller scales?

From Leaf to Plant

At the leaf level, nutrient use efficiency over a leaf's lifetime, cumulative PNUE, can be expressed in terms of photosynthetic nutrient use efficiency, leaf lifespan, and nutrients invested in the leaf and lost at the time of abscission, as follows:

$$Cumulative\ PNUE = \frac{P_S \times Lifespan}{L_N\,(1-RES)} = PNUE \times \frac{Lifespan}{(1-RES)} \qquad (1)$$

where *PNUE* is photosynthetic nutrient use efficiency, and is the ratio of average daily carbon gain to peak foliar nutrient content; *Lifespan* is the leaf's lifespan; and *(1-RES)* denotes the fraction of nutrients not resorbed by the plant prior to leaf abscission (Chapters 1, 3).

At the plant level, nutrient use efficiency is the ratio of total biomass production to total nutrient uptake (Hirose 1975). Total biomass production depends on photosynthetic nutrient use efficiency, total nutrients allocated to leaves, and total leaf

area, minus carbon expended in respiration by non-photosynthetic tissue. Total nutrient uptake is equivalent to the sum of nutrient accrual in biomass, plus nutrients lost in litterfall and via leaching from the crown. Assuming steady state conditions, such that total biomass produced is equivalent to total litterfall biomass and total nutrient uptake is equivalent to total litterfall nutrients (cf Vitousek 1982), and assuming nutrient leaching losses from the crown are negligible (e.g., as found for N, Chapter 4), then plant nutrient use efficiency can be expressed as follows.

$$Plant\ NUE = \frac{NPP}{Uptake} = \frac{(PNUE \times L_N \times SLA \times Leaf\ Biomass) - (R_S \times Non\text{-}Leaf\ Biomass)}{\frac{Leaf\ Biomass}{Lifespan} \times SLA \times L_N\ (1\text{-}RES)} \quad (2)$$

L_N denotes leaf nutrient content on an area basis; *SLA* is specific leaf area; *Leaf Biomass* is the total biomass of leaf tissue; R_S is respiration by non-photosynthetic tissue; and *Non-Leaf Biomass* is the total biomass of non-photosynthetic tissue (Chapter 1).

All terms that contribute to cumulative PNUE at the leaf level reoccur in the expression for nutrient use efficiency at the plant level (equations 1 and 2, Figure 6-1). This suggests that it might be possible to predict plant nutrient use efficiency from a knowledge of leaf nutrient use efficiency. I investigated this in studies of nutrient use efficiency with respect to nitrogen (N) and phosphorus (P) at the leaf (Chapter 3) and plant (Chapter 4) level in three species of tropical trees, *Hyeronima alchorneoides*, *Cedrela odorata,* and *Cordia alliodora*.

With respect to P, nutrient use efficiency at the leaf level followed the pattern *Hyeronima* > *Cedrela* and *Cordia*, and this pattern was repeated at the plant level. With respect to N, as with P, nutrient use efficiency at the leaf level also followed the pattern

Hyeronima > *Cedrela* and *Cordia*, but nutrient use efficiency at the plant level followed the pattern *Hyeronima* > *Cedrela* > *Cordia* (although it was not possible to detect significant differences among them).

What might account for these differences? One explanation for the divergent patterns for N and P observed in comparing nutrient use efficiency of leaves and plants comes from a consideration of processes at the leaf level. A comparison of leaf-level N and P use efficiency presents two different situations. The situation with respect to P is that nutrient use efficiency of the study species is a function of their differences in lifespan and resorption alone, because photosynthetic P use efficiency does not differ among them (Chapter 3). The situation with respect to N, in contrast, is that nutrient use efficiency of the study species is a function of their differences in lifespan, resorption, and photosynthetic N use efficiency (Chapter 3). Therefore, one explanation for the differences between patterns of N and P use efficiency at the leaf and plant levels may be because of differential influences of the components of leaf-level nutrient use efficiency on plant-level nutrient use efficiency. I investigated this hypothesis using a sensitivity analysis, as follows.

As a first step in investigating the effects of components of leaf nutrient use efficiency on plant-level nutrient use efficiency, I calculated the magnitude of the change in plant nutrient use efficiency in response to changes in each of the independent factors (equation 2). Values used for all factors, except respiration by non-leaf tissue, were average values measured for the three study species. The value used for respiration of non-leaf tissue was that of maintenance respiration obtained from Ågren (1996). All independent factors were varied over a range of 50 to 150 percent of their value.

Calculated values of nutrient use efficiency at the plant level were transformed to percent changes from the original average value. The results of this analysis indicated that nutrient use efficiency for this hypothetical "average tree" was very responsive to changes in components of leaf-level nutrient use efficiency, but was less responsive to changes in the other variables (Figure 6-2).

I then investigated the effects of variation in leaf-level factors alone, holding all other factors constant. The approach used follows that of Williams and Yanai (1996): In the first case, only leaf lifespan and resorption were varied through the range of values represented by the three species (cf leaf P use efficiency, where interspecific differences at the leaf level were a function of these two factors alone). Three levels were used for each factor, leading to a total of nine calculations, and the percent change in plant nutrient use efficiency was graphed as a function of changes in nutrient resorption; the lowest value of resorption is representative of *Cordia,* and the highest value of resorption is representative of *Cedrela* and *Hyeronima*. The three lines represent leaf lifespans of the different species (Figure 6-3).

In the second case, leaf lifespan, resorption, and photosynthetic nutrient use efficiency were all varied (cf leaf N use efficiency, where interspecific differences at the leaf level were a function of all three factors). The three levels used for each factor led to a total of 27 calculations (Figure 6-4). As with P, the lowest value of resorption is representative of *Cordia,* and the highest value of resorption is representative of *Cedrela* and *Hyeronima*. The three lines represent leaf lifespans of the different species. Each panel denotes a different level of photosynthetic nutrient use efficiency: the lowest

photosynthetic nutrient use efficiency is representative of *Cordia*, while the highest photosynthetic nutrient use efficiency is representative of *Cedrela*.

For P, the analysis indicated that a combination of high leaf lifespan and nutrient resorption (cf *Hyeronima*) led to a large increase in plant nutrient use efficiency (Figure 6-3). Furthermore, it indicated that a combination of intermediate leaf lifespan and low nutrient resorption (cf *Cordia*) had approximately the same effect on plant nutrient use efficiency as a combination of low leaf lifespan and high resorption (cf *Cedrela*). This result is similar to plant-level P use efficiency measured for the three species, but the relative magnitudes of measured *Cedrela* and *Cordia* P use efficiency (though not different) were the reverse of the calculated outcome.

For N, the analysis indicated that high leaf lifespan and resorption, despite intermediate photosynthetic nutrient use efficiency (cf *Hyeronima*), still resulted in high plant nutrient use efficiency (Figure 6-4). A combination of intermediate leaf lifespan, low resorption, and low photosynthetic nutrient use efficiency (cf *Cordia*) led to a greater reduction in plant nutrient use efficiency compared to the hypothetical average tree than a combination of low leaf lifespan, high resorption, and high photosynthetic nutrient use efficiency (cf *Cedrela*), but the two outcomes were only marginally different. This result differs from plant-level N use efficiency measured for the three species.

Thus, the sensitivity analysis indicated that it may be possible to predict plant-level nutrient use efficiency from leaf-level nutrient use efficiency with respect to P. With respect to N, on the other hand, the sensitivity analysis indicated that leaf-level nutrient use efficiency may not be sufficient to predict nutrient use efficiency at the plant level. What other factors might control differences in N and P use efficiency at the plant level?

One alternative explanation for the divergent patterns for N and P observed in comparing nutrient use efficiency of leaves and plants comes from a consideration of larger scale processes. It was demonstrated for the study systems that soil N availability became progressively limiting over time (Chapter 5). Changes in nutrient availability can have unrelated outcomes for photosynthesis and plant growth. In grasses, for example, it was found that the effects of reduced N availability manifested themselves first as a reduction in whole-plant growth and only secondarily as a reduction in photosynthetic rates (Ranjith and Meinzer 1997). Results from fertilization of N-limited trees along a natural fertility gradient in Hawaii suggest a similar process: increased N led to increased whole-plant growth of *Meterosideros polymorpha*, presumably as a result of greater allocation to leaves, but with no accompanying change in rate of photosynthesis per unit leaf area (Susan Cordell, pers. comm.).

It is possible to envisage a similar situation in the case of the study species. For example, interspecific differences in leaf P use efficiency paralleled differences in plant P use efficiency. On the other hand, interspecific differences in leaf N use efficiency did not parallel differences in plant N use efficiency. With respect to N, this could be due to a reduction in plant growth per unit of N taken up, but without a similar reduction in photosynthesis per unit of leaf N.

From Plant to Ecosystem

At the ecosystem level, nutrient use efficiency is the ratio of net primary productivity (NPP) to the rate of soil nutrient supply:

$$Ecosystem\ NUE = \frac{NPP}{Supply} \quad (3)$$

This expression can be further expanded as follows (Bridgham et al. 1995):

$$Ecosystem\ NUE = \frac{NPP}{Supply} = \frac{NPP}{Uptake} \times \frac{Uptake}{Supply} \quad (4)$$

where the ratio of NPP to nutrient uptake is equivalent to plant nutrient use efficiency (Hirose 1975), and the ratio of uptake to soil nutrient supply is a measure of uptake efficiency (Shaver and Melillo 1984). Analogous to the relationship between nutrient use efficiency of leaves and plants (equation 3), nutrient use efficiency at the plant level is entirely nested within nutrient use efficiency at the ecosystem level (equations 3 and 4, Figure 6-1). Therefore, plant nutrient use efficiency might have important consequences for nutrient use efficiency at the ecosystem level. I compared nutrient use efficiency with respect to N and P at the plant (Chapter 4) and ecosystem (Chapter 5) levels.

With respect to P, nutrient use efficiency at the plant level followed the pattern *Hyeronima* > *Cedrela* and *Cordia*, but nutrient use efficiency at the ecosystem level followed the pattern *Hyeronima* > *Cedrela* > *Cordia*. With respect to N, on the other hand, nutrient use efficiency at the plant level followed the pattern *Hyeronima* > *Cedrela* > *Cordia*, (although it was not possible to detect significant differences among them), while nutrient use efficiency at the ecosystem level followed pattern *Hyeronima* > *Cedrela* and *Cordia*.

Considering the example of N use efficiency, ecosystem nutrient use efficiency was measured over a period of 4 yr during which relative availabilities of soil N and P changed considerably. N availability dropped steadily over the 4 yr, while P availability showed an increasing trend, leading to progressively greater N limitation over time, as

suggested by changes in ratios of foliar N to P—foliar N:P > 16 signals relative P limitation, while foliar N:P < 14 signals relative N limitation (Koerselman and Meuleman 1996, Figure 6-5). Ecosystem N use efficiency was inversely related to N availability for all three species (as is to be expected, since the calculation of ecosystem nutrient use efficiency includes nutrient availability). Nevertheless, there were marked differences among species: nutrient use efficiency of *Cedrela* and *Cordia* did not increase once a certain threshold N availability had been crossed, whereas *Hyeronima* nutrient use efficiency continued to increase with declining N availability (Figure 5-14). It is possible that *Cedrela* and *Cordia*, with their lower plant-level N use efficiencies than *Hyeronima*, have a lower tolerance of reduced N availability. Therefore, a decline in N availability may manifest itself as a reduction in *Cedrela* and *Cordia* productivity before a similar reduction is apparent in *Hyeronima*. Such a reduction in stand level productivity once nutrient availability declines below a threshold value was reported for stands of trees along a fertility gradient in Wisconsin (Lennon et al. 1985). They suggested that the mechanism underlying this observed decrease in productivity, and therefore in ecosystem nutrient use efficiency, was the allocation of scarce N to leaves at the expense of new woody growth. Grubb (1989) made a similar case for declining nutrient use efficiency with declining nutrient availability based on observations of increased proportional allocation to leaves rather than woody tissue in communities along large-scale gradients in soil fertility (Grubb 1977).

An alternative explanation for the observed decline in nutrient use efficiency with declining nutrient availability among ecosystems dominated by the three tree species could lie in changes in relative allocation to above- and below-ground biomass. It is

suggested that plants allocate biomass to the acquisition of resources such that all resources are simultaneously limiting (Bloom et al. 1985). It could be, therefore, that as N became relatively more limiting—first to *Cordia*, and then to *Cedrela*—there was a shift to greater allocation below ground. Thus, ecosystem nutrient use efficiency calculated solely on the basis of aboveground NPP showed a decline, but it is possible that ecosystem nutrient use efficiency calculated based on above and belowground NPP taken together would continue to increase with declining nutrient availability. Ostertag (1998) observed greater belowground NPP in P-limited forests than in N-limited forests. She suggested that nutrient returns per unit of root length invested are likely to be greater under P-limitation than under N-limitation, therefore increased belowground allocation would be selected for in communities that have evolved in P- but not in N-limited environments. Nevertheless, increased belowground allocation may occur in response to N limitation in environments that are not chronically N limited.

An examination of standing above- and below-ground biomass (Figure 6-6) shows that root to shoot ratios actually decline from one year to the next in the *Hyeronima*- and *Cedrela*- dominated systems and in the *Cordia*-dominated polycultures, contrary to the prediction made. In the *Cordia*-dominated monocultures, on the other hand, the ratios of root to shoot biomass remain approximately constant over the 4 yr of the study. This suggests that relative allocation to belowground tissue compared to aboveground tissue is higher in the *Cordia*-dominated monocultures, and partially supports the hypothesis of increasing proportional allocation to belowground tissue in response to declining nutrient availability. Furthermore, these ratios of root to shoot biomass do not take into account the dynamics of allocation to above and belowground

tissue. There may, in fact, be a much greater allocation to belowground tissue than indicated by an examination of standing biomass alone: for example, in a comparison of P-limited and fertilized sites in Hawaii, Ostertag (1998) found as much as a twofold difference in fine root turnover, but with no accompanying change in standing biomass of fine roots.

Nutrient Use Efficiency in Managed Ecosystems

In addition to understanding the links between nutrient use efficiency of leaves, plants, and ecosystems, there are several other considerations important to managing nutrient use efficiency. One of these is the question of nutrient use efficiency in situations where one resource most limits productivity. The other is the suggestion that there may be tradeoffs between the components of nutrient use efficiency.

Nutrient Interactions

Although plants may be simultaneously limited by multiple resources (Bloom et al. 1985), there are instances where one resource may be particularly limiting. The added supply of that most limiting resource can increase the efficiency of use of other resources (de Wit 1992). At the leaf level, Reich and Schoettle (1988) demonstrated, for seedlings of white pine grown in soils of varying fertility, that rates of maximum photosynthesis were not correlated with foliar N. Furthermore, they demonstrated that this departure from the reported photosynthesis-N relationship was due to P limitation. Similarly, it was shown that plantations of *Eucalyptus* grown in combination with a legume had greater P use efficiency at the ecosystem level than *Eucalyptus* grown alone (Binkley et al.1992).

They attributed this to increased ecosystem productivity on account of greater availability of N returned in *Albizzia* (*Paraserianthes*) litter.

Other such increases in resource use efficiency with the supply of the most limiting resource are reported from experiments in intensively farmed systems (de Wit 1992), but may have equal applicability in low-input farming systems. Thus, although achieving a high efficiency of nutrient use is most imperative in situations where the use of fertilizers is not always an option, the application of a small amount of fertilizer can greatly improve the returns on all other available resources.

The Productivity-Nutrient Conservation Tradeoff

A recurring theme in the discussion of nutrient use efficiency is the idea of tradeoffs between productivity per unit of nutrient acquired, and the effectiveness with which acquired nutrients are retained. This tradeoff was explicitly stated by Berendse and Aerts (1987) in the context of plant nutrient use efficiency. They proposed that high-resource environments select for plants that have high productivity per unit of nutrient acquired at the expense of longer retention times of acquired nutrients, and the converse, that low-resource environments favor longer nutrient retention times, but that this may be at a cost to productivity.

The tradeoff between the components of nutrient use efficiency at the plant level has parallels at the leaf and ecosystem levels. For individual leaves high photosynthesis per unit of foliar nutrient content is associated with rapid leaf and nutrient turnover. On the other hand, long-lived leaves lead to longer nutrient retention, but they may have lower photosynthetic capacity per unit of foliar nutrient due to allocation of nutrients to other functions, such as leaf maintenance and defense (Field and Mooney 1986).

Similarly, at the ecosystem level, high nutrient use efficiency may be driven either by high productivity per unit of soil nutrient supply (e.g., as exemplified by the systems in this study, Chapter 5), or by greater nutrient storage in the soil (e.g., in pine plantations in Puerto Rico, as demonstrated by Silver et al. [1996]), which may eventually lead to reduced rates of productivity.

Given the tradeoffs between the components of nutrient use efficiency, how can we aim for optimal nutrient use efficiency? One way may be an optimization in time: It is possible to envision a succession in which short-lived species having high productivity and rapid biomass accumulation, are followed by species that are longer-lived, but grow more slowly. The first wave of species rapidly accrues nutrients in biomass, for instance, immediately following land clearing, and prevents them from being leached from the system (e.g., the role played by pin cherry in northern hardwood forests, as proposed by Marks [1974]). In time they are succeeded by the next wave of species. An alternative scenario could be on highly degraded soils, for instance, where the first wave of succession might include species that have low productivity but a high ability to conserve nutrients. In time, they are succeeded by more productive species, as nutrient cycles are restored.

There may also be a case for optimizing productivity and nutrient conservation in space. A possible scenario is an agroforestry system with an overstory of species with rapid stem growth that dominate a site, but do so at the expense of complete resource capture (Tilman 1988, Haggar and Ewel 1997). In combination with an understory of species that better conserves resources, although at the expense of high productivity, such a system could achieve high total nutrient use efficiency at the ecosystem level.

Summary

The results indicate, therefore, that, although nutrient use efficiency at smaller scales is nested within nutrient use efficiency at the scales above, at each level nutrient use efficiency may be subjected to top-down control by larger scale processes. Thus, for example, although plant P use efficiency was predicted by leaf P use efficiency, plant N use efficiency could not be predicted based on leaf N use efficiency alone. Nevertheless, the outcome of the interaction between nutrient use efficiency and the top-down factors controlling it may be modified by nutrient use efficiency at smaller scales. For example, at the ecosystem level, nutrient use efficiency across all species was related to soil nutrient availability, but the individual responses of ecosystems dominated by the different tree species depended on their plant-level nutrient use efficiencies. The other result that emerged was that the relationship between nutrient use efficiency at several scales may be a function of the nutrient under consideration. For example, leaf and plant P use efficiency appeared to be related, while leaf and plant N use efficiency did not.

Another consideration highlighted, even in the brief snapshot-in-time over which this study was conducted, was the importance of temporal changes in nutrient availability for nutrient use efficiency at the plant level, with consequences for nutrient use efficiency at the ecosystem level. Changes in availability of a particular nutrient can affect not only the efficiency with which that particular nutrient is used at several scales, but also the efficiency of use of other resources (Reich and Schoettle 1988, de Wit 1992, Binkley et al.1992). Therefore, an understanding of the effects of cross-scale linkages in nutrient use efficiency, as well as the effects of nutrient interactions on nutrient use efficiency, are crucial in enabling us to achieve the optimum mix of productivity and nutrient

conservation in changing environments, with only the minimum possible reliance on external fertilizer inputs.

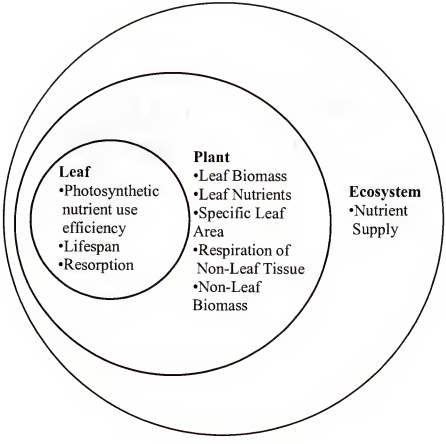

Figure 6-1. A schematic of the proposed links between the components of nutrient use efficiency at leaf, plant, and ecosystem scales. Leaf nutrient use efficiency is nested within plant nutrient use efficiency; plant nutrient use efficiency, in turn, is nested within ecosystem nutrient use efficiency. (See equations 1 to 4 in text.)

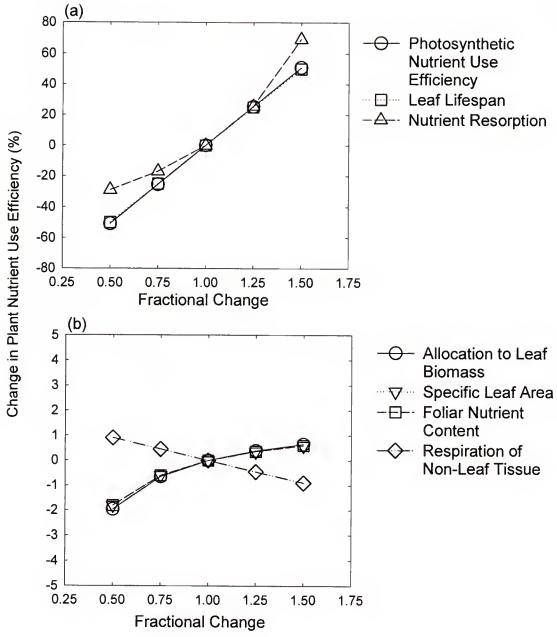

Figure 6-2. Change in plant nutrient use efficiency in response to changes in the components of plant nutrient use efficiency. Each factor was varied separately, holding all others constant. The results of variation in photosynthetic nutrient use efficiency, leaf lifespan, and resorption are shown in panel (a), the results of variation in all other factors are shown in panel (b). (Note differences in the y-axis scale between [a] and [b].)

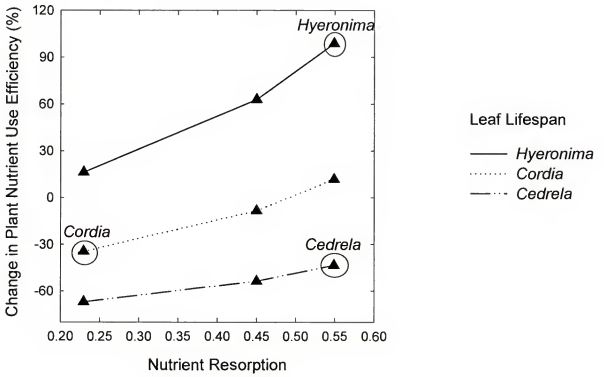

Figure 6-3. Change in plant nutrient use efficiency when resorption and leaf lifespan are varied together. Resorption of 0.23 corresponds to phosphorus resorption by *Cordia*, resorption of 0.55 corresponds to phosphorus resorption by *Cedrela* and *Hyeronima*.

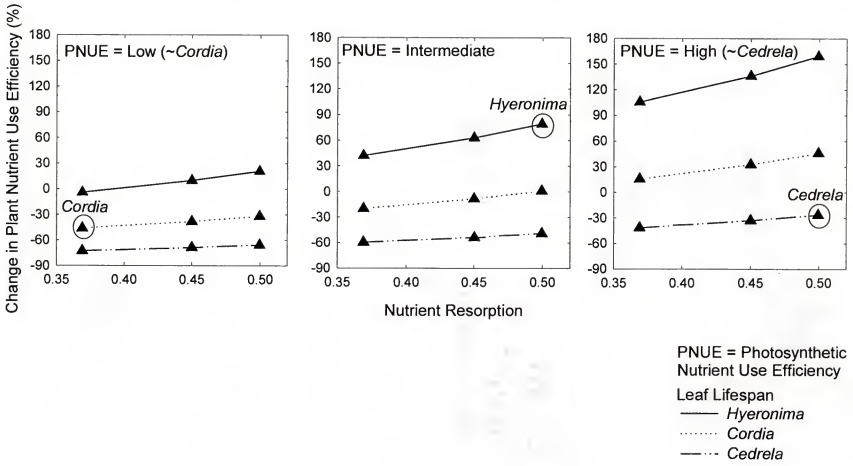

Figure 6-4. Changes in plant nutrient use efficiency when resorption, leaf lifespan, and photosynthetic nutrient use efficiency are varied together. Resorption of 0.37 corresponds to nitrogen resorption by *Cordia*, and resorption of 0.49 corresponds to nitrogen resorption by *Cedrela* and *Hyeronima*.

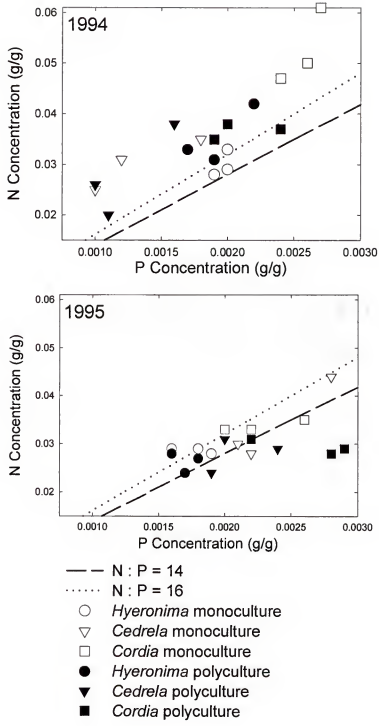

Figure 6-5. Ratios of foliar N to P in 1994 and 1995. Foliar N and P were measured on disks of leaf lamina tissue. Points represent composite samples of three leaves sampled from each of five trees. The lines for N:P = 14 and N:P = 16 denote the thresholds for relative N and P limitation, respectively (after Koerselman and Meuleman 1996).

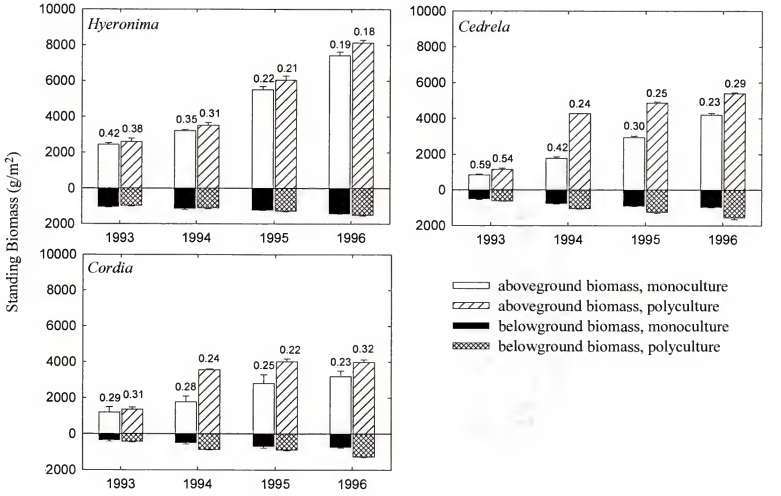

Figure 6-6. Standing above- and below-ground biomass in systems dominated by the three tree species. Values are means (standard errors) of three blocks. Numbers indicate root to shoot ratios.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that it in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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